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ScienceDirect
Theoretical Population Biology 71 (2007) 267–277
Theoretical Population Biology
www.elsevier.com/locate/tpb

Spatial patterns and coexistence mechanisms in systems with unidirectional flow

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Received 30 November 2005
Available online 15 December 2006

Abstract

River ecosystems are the prime example of environments where unidirectional flow influences the dispersal of individuals. Spatial patterns of community composition and species replacement emerge from complex interplays of hydrological, geochemical, biological, and ecological factors. Local processes affecting algal dynamics are well understood, but a mechanistic basis for large scale emerging patterns is lacking. To understand how these patterns could emerge in rivers, we analyze a reaction–advection–diffusion model for two competitors in heterogeneous environments. The model supports waves that invade upstream up to a well-defined "upstream invasion limit". We discuss how these waves are produced and present their key properties. We suggest that patterns of species replacement and coexistence along spatial axes reflect stalled waves, produced from diffusion, advection, and species interactions. Emergent spatial scales are plausible given parameter estimates for periphyton. Our results apply to other systems with unidirectional flow such as prevailing winds or climate-change scenarios.

Keywords: Spatial competition; Periphyton communities; Invasion waves; Coexistence; Environmental heterogeneity; Reaction–advection–diffusion equations

1. Introduction

One defining feature of river ecosystems is the presence of a strongly unidirectional flow. This flow induces a heavy bias in the dispersal of individuals such as algae, invertebrates, and stream insects. The question *how* a population can persist in rivers despite the flow-induced washout has been termed the "drift paradox" (Müller, 1982), and has been addressed in recent modeling papers (Lutscher et al., 2005; Pachepsky et al., 2005; Speirs and Gurney, 2001). In this paper, we address the question *where* in a river a species can persist, given natural spatial variation in resource levels. We also study how unidirectional flow influences the outcome of competition, and in particular how it may mediate coexistence of two competitors.

We formulate our model for algal communities in rivers, however, our results apply to many other scenarios of flow-through systems. Coastlines with long-shore currents present a similar environment (Gaylord and Gaines, 2000), as do plug-flow reactors, which have been used as models for the gut (Ballyk and Smith, 1999). Plants with windborn seeds in valleys with prevailing wind directions face a similar "wash-out" problem. Finally, the pole-ward movement of temperature isoclines due to global warming induces unidirectional "flow" by a change of reference frame (Potapov and Lewis, 2004).

Algal communities in river ecosystems are highly dynamic. Species composition changes significantly over time at a particular spatial location in response to temporal variation in local nutrient concentrations and herbivore levels (Alvarez and Peckarsky, 2005; Hillebrand, 2002;

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0040-5809/$ - see front matter © 2006 Elsevier Inc. All rights reserved.
doi:10.1016/j.tpb.2006.11.006

Henry and Fisher, 2003; Lamberti et al., 1989; Pringle, 1990), and physical disturbances (McCormick and Stevenson, 1991; Peterson and Stevenson, 1992; Robinson and Minshall, 1986). Larger scale spatial patterns in community composition and species replacement emerge from these local interactions, and some general features of these patterns have been catalogued (Hill et al., 2000; Lavoie et al., 2003; Snyder et al., 2002; Wright and Li, 2002). While there has been extensive work done to understand processes at local spatial scales (e.g. Hillebrand, 2002 and citations above), there has been little work testing ideas as to how larger-scale spatial patterns are produced. For example, larger-scale empirical patterns based on the "River Continuum" (RCC) (Vannote et al., 1980) or "Serial Discontinuity Concepts" (SDC) (Ward and Stanford, 1983) have been compiled. The RCC is often used to predict the community composition of biotic groups as one moves down from headwater streams to larger rivers. It assumes that benthic community composition reflects the relative contribution of carbon loading from terrestrial versus in stream sources. The SDC modifies the RCC by explicitly considering the direct (e.g. flow modification) and indirect (nutrient cycling) hydrological effects of dams on modifying the relationship between external and internal loading, as well as the environmental influences on community composition. However, the mechanistic basis for these patterns is poorly understood. Important linkages among hydrology, biogeochemistry, ecological interactions, and population processes have been established (Biggs et al., 1998; Dent et al., 2002; Fisher et al., 1998; Woodward and Hildrew, 2002), but general explanations for both the temporal and spatial dynamics of algal species need to be elucidated and tested in river systems.

Recent experimental work investigating mechanisms producing basin-scale patterns in algal community dynamics (Peterson, 1996; Cardinale et al., 2005) highlights the role of dispersal mechanisms interacting with local processes, either following disturbance or along nutrient gradients. To understand how these mechanisms give rise to spatial patterns and temporal dynamics, we need a framework that incorporates ecological interactions and dispersal, along with advective flow down river. Table 1 summarizes the models used to understand periphyton (benthic algae) dynamics in streams and rivers and their biological and physical assumptions. These models typically include ecological interactions and the effect of advective flow but not dispersal. The situation is different for terrestrial systems where extensive work on spatial coexistence mechanisms has been undertaken (Amarasekare et al., 2004) involving diffusion, but advective flow was not considered for obvious reasons.

In this paper, we use a strategic approach to understand how spatial competitive outcomes among algal species are influenced by environmental heterogeneity in the presence of advection and diffusion. Our goal is to understand how competing species invade and coexist in space under different environmental scenarios. The mathematical formalism we use abstracts much of the biology of the competitors into a phenomenological description of the effects of changes in species density on growth rates of competitors.

In the next section, we present our model that consists of two reaction–advection–diffusion equations coupled by Lotka–Volterra interaction terms. The analysis proceeds in three steps. At first, we consider only a single species in a heterogeneous environment. We introduce the notion of an *upstream invasion limit*. This point in space can be computed explicitly from the model parameters. Numerical simulations reveal that an upstream-invading wave gets stalled at this point. Secondly, we investigate numerically how two competitors can coexist in a homogeneous environment. It turns out that boundary effects at the upstream boundary may lead to coexistence. Finally, we extend the definition of upstream invasion limits to the two-competitor case and show that coexistence can occur if the better competitor has its invasion limit downstream from that of the weaker competitor. In the discussion, we use published data to show that the spatial scales over which we expect coexistence to occur are reasonably large.

2. Model description

We start by focusing on the effect of competition on the abundance and distribution of species in rivers. While competitive dynamics are well studied in ecology, the interaction of competitive dynamics between species and the physical flow in a river, via diffusion and advection in the river is complex. As we will show in this paper, this can produce a rich and biologically interesting set of competitive outcomes that relate directly to river ecosystems.

While recognizing that competitive interactions in rivers are typically mediated via resource limitations (Son and Fujino, 2003), our approach is to take the simplest possible model for competition that remains biologically interesting, that of Lotka–Volterra competition. To this we add diffusive (random) and advective (directed) flow, as well spatial variation in intrinsic growth rates (reflecting changing conditions for growth in the river system).

We consider two competing species in a river and denote $N_{1,2}(t,x)$ as their respective densities at time $t \geqslant 0$ and downstream location x. The equations read

$$\begin{aligned}\frac{\partial N_1}{\partial t} &= D_1\frac{\partial^2 N_1}{\partial x^2} - V_1\frac{\partial N_1}{\partial x} + N_1(R_1(x) - A_{11}N_1 - A_{12}N_2),\\ \frac{\partial N_2}{\partial t} &= D_2\frac{\partial^2 N_2}{\partial x^2} - V_2\frac{\partial N_2}{\partial x} + N_2(R_2(x) - A_{21}N_1 - A_{22}N_2),\end{aligned} \tag{1}$$

where $R_i(x)$ are the respective growth rates, A_{ij} the inter- and intraspecific competition coefficients, D_i are the diffusion coefficients and V_i the flow speeds. We assume that $V_1, V_2 > 0$ so that the flow is from left to right. Whereas flow speed might remain constant downstream or increase slightly in natural systems (Leopold, 1962), it is

Table 1
Modeling approaches for periphyton

Modeling area reference	Approach	State variables	Processes considered	Major results
Lotic ecosystems	Single-reach model	Biomass of several functional groups	Production, respiration, grazing, shredding, collecting, (in-) vertebrate predation	Maximum biomass at intermediate flow velocities
McIntire et al. (1996)	Ordinary diff. Eq.	Nutrients, dissolved organic matter	Light, flow, temperature	Consumer biomass is indicator for productivity of the system
	Difference Eq.			Complex processes lead to some counterintuitive outcomes
Diatom migration	Water column sampling	Biomass of each species	Emigration, immigration, growth, temperature	Emigration and immigration quantified for each species
Stevenson and Peterson (1991)	Difference Eq.			Variation of abundance in water column explained
Nutrient-periphyton dynamics	Single-reach model	Nutrient concentration in each compartment	Uptake, growth, remineralization, flow, export	Algal grow is self-limited
Mulholland and DeAngelis (2000)	Flow and benthos			Hyporheic zone is important factor
	Ordinary diff. Eq. Downstream coupling			Nutrient uptake length calculated
Periphyton mat dynamics	Complex simulation model	Biomass of algae	Uptake, growth, mortality, detachment, respiration, shading, temperature	Succession from non-filamentous to filamentous
Son and Fujino (2003)	Ordinary diff. Eq.	Length of filaments		Light and detachment quantified
	Partial diff. Eq.	External and internal Nutrient concentration		
River-scale modeling	Complex simulation model, 40 km reach	Biomass of phytoplankton and periphyton	Carbon-, nutrient-, and oxygen cycling, transport, diffusion of nutrients and phytoplankton	Integrative model of highly complex processes
Flipo et al. (2005)	Ordinary diff. Eq.	Concentration of nutrients and oxygen		Periphyton is predominant in nitrification and contributed greatly to carbon standing stock and downstream export
	Partial diff. Eq.			

In each category we only list the most recent reference for the model type or author group. All models contain population dynamics of periphyton and are parameterized from experiments. Flow is included as an additional loss term. Only the model by Stevenson and Peterson (1991) considers emigration and immigration explicitly, none of the others contains spatial movement of periphyton. The models by McIntire et al. (1996) and Stevenson and Peterson (1991) are non-spatial, Mulholland and DeAngelis (2000) and Son and Fujino (2003) consider both, non-spatial and spatial models, the approach by Flipo et al. (2004) is explicitly spatial and, as the only one in the list, includes hydrodynamics.

unclear whether the same holds when large amounts of water are extracted from rivers for agricultural use or human consumption. For simplicity, we consider a spatially constant speed here.

We would like to point out that the interaction terms in the model formulation are somewhat different from the standard notation. Usually, the growth rates R_j are factored out of the brackets and the interaction coefficients have dimension $(\text{density})^{-1}$, whereas in our case the A_{ij} have dimension $(\text{density} * \text{time})^{-1}$. Mathematically, the two formulations are, of course, equivalent, but the one presented here and elsewhere (Potapov and Lewis, 2004; Shigesada et al., 1986) has certain advantages for our purposes. For example, the formulation is consistent with $R_j < 0$. More importantly, for a logistic equation in a spatially varying environment, one has the choice of varying the intrinsic growth rate, or the carrying capacity or both. Since we aim for a simple model, we link the two and thereby reduce the number of parameters, because the carrying capacities are now given by $K_j = R_j/A_{jj}$. For convenience, we can rewrite the reaction term in (1) of species 1, say, as

$$R_1 N_1 \left(1 - \frac{N_1 + \alpha N_2}{K_1}\right), \tag{2}$$

where $\alpha = A_{12}/A_{11}$, which relates our choice of parameters to the more commonly used form of the equations. In particular, the parameters $A_{ij}, i \neq j$ are simply multiples of the commonly used competition coefficients (Britton, 2003).

The case where growth rates $R_{1,2}$ are constant was studied mathematically by Potapov and Lewis (2004), in particular when the river is very long (mathematically speaking, an unbounded domain). There, the coupled growth and dispersal can lead to population spread in space. The invasion speed at which the population spreads is a key quantity that will play a role later in this paper. It is easiest to first consider the case for (1) with a single species and no advective flow ($N_2 = 0$ and $V_1 = 0$). This is simply logistic growth with random dispersal, or the so-called Fisher equation, which has invasion speed $2\sqrt{D_1 R_1}$ (Fisher, 1937). If $V_1 \neq 0$ the invasion speed in the direction of the flow is given by $2\sqrt{D_1 R_1} + V_1$, whereas the speed in the opposite direction is given by $2\sqrt{D_1 R_1} - V_1$. In particular, the invasion does not move against the flow when $V_1 > 2\sqrt{D_1 R_1}$ (Pachepsky et al., 2005).

In two-species competition models, one can study the case where a superior competitor (say species 1) outcompetes the other competitor, and spreads spatially into the (infinite) region previously occupied by species 2. For Lotka–Volterra competition as above, with $V_{1,2} = 0$, the speed at which the weaker competitor retreats is identical to the speed at which the stronger one advances. This replacement process occurs at speed

$$2\sqrt{D_1(R_1 - R_2 A_{12}/A_{22})} \tag{3}$$

provided the following two conditions are satisfied (Lewis et al., 2002)

$$\frac{D_2}{D_1} \leqslant 2, \quad \frac{(A_{12}A_{21}/A_{11}A_{22}) - 1}{1 - (A_{12}R_2/A_{22}R_1)} \leqslant \frac{R_1}{R_2}\left(2 - \frac{D_2}{D_1}\right). \tag{4}$$

These conditions are sufficient but not necessary as numerical simulations show. However, the spreading speed can be much larger if the conditions are violated (Lewis et al., 2002). In all simulations presented below, conditions (4) are satisfied, and hence the spreading speed of the better competitor into the domain occupied by the weaker competitor is given by (3).

A more accurate depiction of a river is a body of water of finite length L. We can consider Eqs. (1) on a bounded domain $[0, L]$ where, of course, population spread cannot continually happen at constant speed. We consider $x = 0$ to be the top of the river where individuals neither leave nor enter (zero flux). In contrast to previous modeling approaches (Speirs and Gurney, 2001; Pachepsky et al., 2005) we consider a river where the downstream boundary at $x = L$ is "far away," i.e., has no influence on upstream processes. These two assumptions are encapsulated in the so-called Danckwerts boundary conditions (Ballyk et al., 1998)

$$\begin{aligned} &D_i \frac{\partial N_i}{\partial x} - V_i N_i = 0, \quad x = 0, \\ &\frac{\partial N_i}{\partial x} = 0, \quad x = L, \ i = 1, 2. \end{aligned} \tag{5}$$

The first of these boundary conditions describes zero flux at the top of the river, and the second describes zero variation in population density with space at the downstream boundary. For a derivation and discussion of these boundary conditions from a random-walk perspective, see Lutscher et al. (2006). From here on, we make the following simplifying assumptions:

1. Diffusion and flow speeds are the same for both species, $D_1 = D_2 = D, V_1 = V_2 = V$.
2. Growth rates are linear and non-decreasing, and $R_2/R_1 = \rho =$ const., i.e.,

$$\begin{aligned} &R_1(x) = R_U + (R_L - R_U)x, \quad R_U \leqslant R_L, \\ &R_2(x) = \rho R_1(x), \end{aligned} \tag{6}$$

where the indices U, L stand for the upper and lower end of the river section.

The main focus in Sections 3 and 4 below is on numerical results, their biological interpretation and significance. Here we briefly give some background on analytical results and the numerical methods used. In the case of a single equation (e.g., $N_2 = 0$) and positive initial data, all solutions converge to a unique stable equilibrium. Depending on parameter values, this equilibrium is either zero (if zero is locally stable) or positive (if zero is unstable). This result follows from the shape of the reaction term (logistic growth) and the fact that the equation satisfies a maximum principle. As a consequence, the outcome of numerical simulations is independent of the chosen initial conditions. The 2-species system is a so-called "monotone system" (Smith, 1995). When parameters are chosen such that either species can invade the other at equilibrium, the theory of monotone systems predicts that there is a coexistence equilibrium, but it may not be unique (Smith, 1995). Therefore, the final outcome of simulations might depend on initial values, however, we studied the full system (1) numerically for a wide range of initial data, and found again that the final outcome is independent of initial values. (The outcome does, of course, depend on parameter values.) For monotone initial values, solutions formed invading or retreating waves. Since neither the qualitative behavior nor the final outcome of the simulations depends on the initial location of the species, we chose to illustrate the results using initial conditions that allowed most clearly to observe the different processes and time scales involved. For numerical simulations, we chose an unconditionally stable implicit finite-difference scheme. Derivatives were approximated by finite differences, backward in time, central in space for the diffusion term, and upwind for the advection term (Strickwerda, 1989).

For numerical simulations we introduced the non-dimensional quantities

$$\begin{aligned} &t' = t \max_x R_1(x) = tR_L, \quad x' = \frac{x}{L}, \\ &d_i = \frac{D_i}{L^2 R_L}, \quad v_i = \frac{V_i}{LR_L}, \quad n_i = \frac{A_{ii}N_i}{R_L}. \end{aligned} \tag{7}$$

Then the non-dimensionalized system is then given by

$$\frac{\partial n_1}{\partial t} = d_1 \frac{\partial^2 n_1}{\partial x^2} - v_1 \frac{\partial n_1}{\partial x} + n_1(r_1 - n_1 - a_{12} n_2),$$
$$\frac{\partial n_2}{\partial t} = d_2 \frac{\partial^2 n_2}{\partial x^2} - v_2 \frac{\partial n_2}{\partial x} + n_2(r_2 - a_{21} n_1 - n_2), \qquad (8)$$

where now

$$r_i(x) = \frac{R_i(x)}{R_L}, \quad a_{ij} = \frac{A_{ij}}{A_{jj}}. \qquad (9)$$

We used some analytical and some numerical methods to compare the effects of the downstream boundary conditions (5) chosen here to the "hostile" boundary conditions $N_i(t, L) = 0$ used elsewhere (Speirs and Gurney, 2001; Pachepsky et al., 2005). The qualitative differences occur only at the downstream end for long enough domains, where the solutions are forced to zero with hostile conditions. If the domain is long enough to support the populations, then the upstream end is not affected by the downstream boundary conditions. The critical domain size for hostile conditions is larger than for the Danckwerts conditions.

3. Results

3.1. Single species

If only one species is present, and growth is constant in space, i.e., $R(x) = R$, Eqs. (1) reduce to a single equation that was analyzed by Speirs and Gurney (2001) and Pachepsky et al. (2005), see also Murray and Sperb (1983) for a more general mathematical treatment in higher space dimension. Their main results in the present context are that, if the stream is arbitrarily long, the species can invade in the upstream direction if and only if the *invasion condition* $V < 2\sqrt{DR}$ is satisfied. Upstream invasion occurs in the form of a traveling wave, moving against the flow at constant speed. When the river becomes shorter, the total amount of habitat available to the species is reduced. Speirs and Gurney (2001) showed that there is a *critical domain size*, a length of river that is so short that the species cannot survive any further reduction of habitat.

We investigate the case when the growth rate varies spatially. We shall not be concerned whether the species can persist at all but rather where it will be present. We consider a river long enough to exceed the critical domain size where the growth rate varies spatially in such a way that the invasion condition holds at the bottom of the stream but is violated at the top. Then the monotonic increase in growth rate with increasing distance downstream implies that there is a unique point x^* in the domain where

$$V = 2\sqrt{DR(x^*)}. \qquad (10)$$

The resulting behavior is summarized in the following points and illustrated in Fig. 1.

1. The species persists with near-zero density at the top and almost carrying capacity at the bottom.

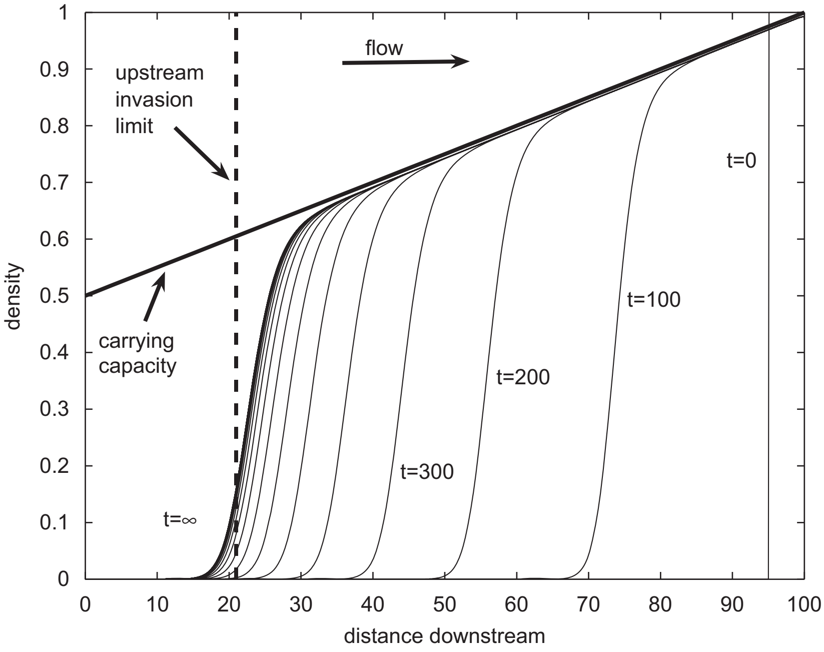

Fig. 1. Invasion process and steady state for a single species in a resource gradient. The flow is from left to right. The initial density ($t = 0$) is located downstream. The profile of the invasion front is plotted every 100 time units. As the front approaches the invasion limit $x^* = 21$ (10), it slows down until it comes to a halt. Upstream the density is almost zero, downstream the density is almost the carrying capacity. The transition between the two states is very steep, much steeper than the gradient in the carrying capacity. The unscaled parameters are $L = 100, D = 1, R_U = 1, R_L = 2, V = 2.2$. In the plot, the densities are scaled to unity.

2. The location of the transition is predicted by the *invasion limit* x^*.
3. If the species is initially located at the downstream end, then it spreads upstream in a wavefront that stalls at the invasion limit.

The steepness of the transition between the two states depends on the parameters. The steepness increases as D decreases provided the product $DR(x^*)$ is held constant so that the invasion limit is fixed. We explored several shapes of non-linear spatially varying growth rates $R(x)$, all monotone increasing so that the upstream invasion limit x^* is well-defined. In all cases, we observed the same qualitative behavior as in the case for linearly increasing growth rates described above.

3.2. Competing species

The non-spatial competition model allows for three different outcomes (coexistence, competitive exclusion, founder control), depending on parameters. We concentrate on the case where species 1 outcompetes species 2 in the non-spatial model, but species 2 has the higher growth rate at low densities, i.e., $R_2/R_1 = \rho > 1, A_{12}\rho < A_{22}, A_{21} > \rho A_{11}$. These conditions depend only on the ratio ρ of the growth rates and are therefore independent of spatial location.

In the homogeneous spatial model with constant growth rates, the outcome of spatial movement and competition depends on the magnitude of the flow speed. For small flow speed, species 1 invades all the way to the upstream boundary, $x = 0$, at a density close to carrying capacity.

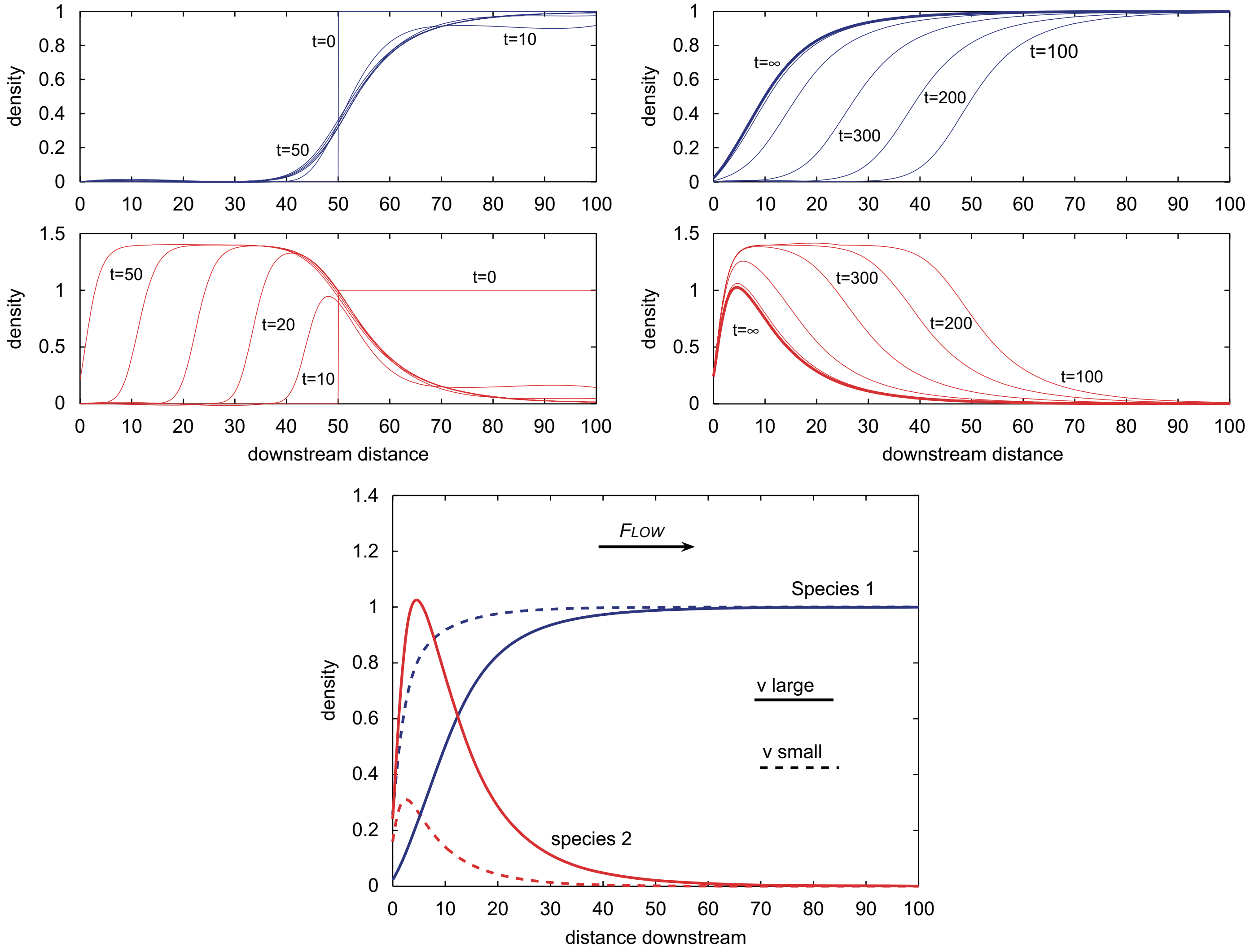

Fig. 2. Time evolution and steady states for two competing species in a homogeneous environment. Initially, both competitors occupy the downstream half of the domain at equal density, but the final outcome is independent of the initial values as long as both species are present. The upper left panels show how within the first 50 time units, species 2 forms an upstream moving front whereas species 1 outcompetes species 2 downstream. The panel on the right shows how subsequently species 1 invades upstream, but much slower than species 2 initially. The third panel on the bottom shows steady state distributions for the two species for two different values of flow speeds where coexistence is possible. For larger flow speed, species 2 occupies more space (solid line). The parameters are $L = 100, D = 1, R_U = R_L = 1, \rho = 1.4, A_{11} = A_{22} = 1, A_{12} = 0.5, A_{21} = 1.5$. The larger flow speed if $V = 1.2$ (also upper panels), the smaller one is $V = 0.8$.

Species 2 goes extinct as predicted by the non-spatial model. At intermediate speeds, coexistence is possible in a boundary layer near the upstream boundary, because the density of species 1 and hence its effect on species 2 is small near the upstream boundary. The coexistence region grows with increasing flow speed. For higher speeds, the competitive outcome is reversed as species 2 persists in the whole domain whereas species 1 gets washed downstream, even though the flow speed would allow persistence in the absence of species 2. If the speed is so large that the invasion condition for species 2 is violated, then both species go extinct.

Fig. 2 depicts how in the case of intermediate flow speeds both species invade upstream. Species 2 spreads faster initially but is being outcompeted downstream by species 1. The upstream spread of species 1 is slower, but the population reaches the upper end of the stream eventually and allows only a small region of coexistence with the inferior competitor near the boundary. Potapov and Lewis (2004) investigated the steady states of a similar system in much more detail.

When growth rates vary spatially, each species has its invasion limit in the absence of the competitor, denoted by $x^*_{1,2}$ and given implicitly by (10). Due to the higher growth rate for species 2, the invasion limit of species 2 is upstream of that of species 1, i.e., $x^*_2 < x^*_1$. There is a second invasion limit for each species, obtained by fixing the density of the competitor at its single-species carrying capacity to find a reduced growth rate $R_i - A_{ij}\bar{N}_j$, with $\bar{N}_j = R_j/A_{jj}$. This second invasion limit is denoted by x^{**}_i and defined implicitly by

$$V = 2\sqrt{D[R_i(x^{**}_i) - A_{ij}\bar{N}_j(x^{**}_i)]}. \tag{11}$$

This definition reduces to (10) in the absence of the other species ($A_{ij}\bar{N}_j = 0$). Because competition has the effect of reducing net growth rates, the single-species invasion limit is upstream of the invasion limit with the competitor at carrying capacity, i.e. $x^*_i < x^{**}_i$.

Fig. 3 shows the resulting behavior of the two competing species under such heterogeneous environmental conditions. Initially, both species are located downstream. The weaker competitor develops a fast moving front that stalls at its invasion limit, x^*_2, as in the single species case. Downstream, the better competitor drives the weaker one to extinction and slowly moves upstream in a monotone wave. This wave stalls far downstream from the single-species invasion limit, x^*_1, namely at the competition-reduced invasion limit, x^{**}_1. At the resulting steady state, there is a spatial zone of coexistence of the two species. In contrast to the coexistence zone in the homogeneous environment above, this zone is not a boundary effect but occurs around the reduced invasion limit of species 1. To summarize:

1. Species 2 spreads upstream in form of a wave that stalls at the invasion limit x^*_2.
2. Species 1 does not reach its invasion limit x^*_1 but only reaches the reduced limit x^{**}_1.

The question of what controls the steepness of the transitions between the states becomes more difficult to answer in this case since more locations and parameters are involved. We concentrate on the front of species 1, where we vary parameters in such a way as to fix the invasion limit x^{**}_1. For increasing D (and therefore decreasing R) the front becomes less steep. Varying the gradient of R while

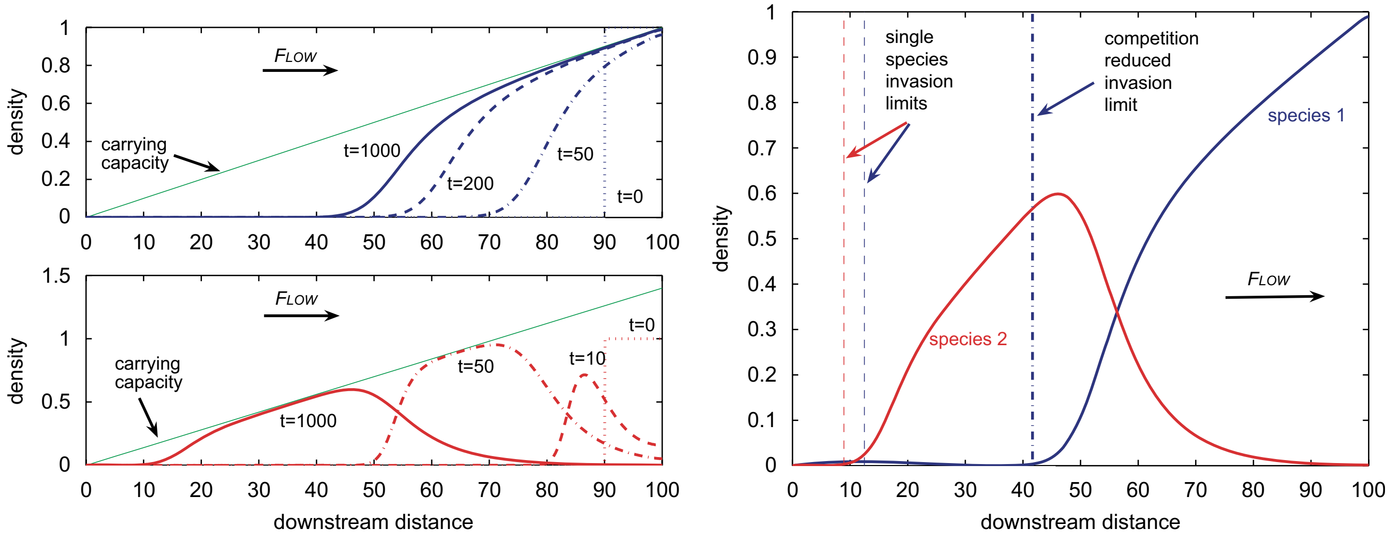

Fig. 3. Invasion of two competitors as in Fig. 2 but in an environment with resource gradient similar to Fig. 1. The two panels on the left show how the two species spread upstream from their initial downstream location. As in Fig. 2, the weaker competitor spreads much faster initially, and the better competitor takes a long time to invade and partially replace its opponent. These two different time scales are reflected in the times chosen to plot the densities. The steady state in the right panel shows that even though the single-species invasion limits are close together, only the weaker competitor can become established upstream. The better competitor reaches its reduced invasion limit. The parameters are $L = 100, D = 1, R_U = 0, R_L = 2, \rho = 1.4, V = 1$, and competition parameters as above.

keeping D fixed has no visible effect on the steepness of the front.

4. Discussion

By integrating local growth and interaction with longitudinal transport and diffusion, we identify a novel approach to understanding processes and patterns in stream ecology. We illustrate this approach using a simple model for one single or two competing species. The major results are the emergence of an upstream invasion limit of a species and two mechanisms of coexistence of competitors along the spatial domain.

4.1. *Invasion limits and stalled waves*

The model not only predicts under which conditions on diffusion, flow and growth rates a species can persist in a certain stream reach as was done before (Speirs and Gurney, 2001; Pachepsky et al., 2005), but it also predicts the location of the upstream limit where a species can persist in a heterogeneous environment. This limit is defined formally as the spatial location where the upstream invasion speed in a corresponding homogeneous environment is zero. Numerical simulations reveal that at this limit there is a sharp transition from almost zero to high density that emerges from a stalled wave. Analytical investigations on the steepness of the transition and the rate at which zero and the positive steady state are approached spatially are currently underway. Since the model is based on the diffusion equation, the steady state is everywhere positive unless it is identically zero. For ecological purposes, however, the density above the invasion limit is effectively zero.

Our model explicitly considers how colonization and local processes combine to produce spatial dynamics. There are few studies that consider "open systems" (Nisbet et al., 1997) and even fewer that explicitly consider the importance of a colonizer pool (Stevenson and Peterson, 1991). While the idea of an upstream invasion might sound strange at first, given that species such as algae and invertebrates are subject to water currents, we want to point out that advection–diffusion equations appear to capture the process of particle transport in flow environments reasonably well (Bencala and Walters, 1983).

4.2. *Coexistence mechanisms*

The analysis of the spatial Lotka–Volterra competition model in homogeneous and heterogeneous environments reveals two inherently spatial mechanisms for coexistence in the case where the competition coefficients indicate competitive exclusion in the corresponding non-spatial system. As in the previous section, we always refer to species 1 as the better competitor whereas species 2 has the higher growth rate.

The first mechanism occurs in the homogeneous environment and is identified as a boundary effect. The flow at the upstream boundary pushes both competitors downstream and decreases their density near the boundary. The small density of species 1 has only a small effect on species 2. This boundary layer is small for small flow velocities so that species 1 still excludes species 2. For intermediate velocities, however, species 2 can coexist at the upstream boundary, and for higher velocities the competitive outcome is even reversed so that species 2 alone persists. Conversely, this suggests that decreasing flow rates, e.g. due to water extraction, may lead to changes in species composition through upstream invasion of superior competitors. This effect may be compounded by concomitant changes in nutrient concentration with decreased flow rate. Potapov and Lewis (2004) present an in-depth analysis of similar phenomena in the context of population spread under climate shift.

This boundary effect described above depends on the presence of flow and is therefore different from previously established results where diffusion induced boundary loss facilitates coexistence (Fagan et al., 1999).

The second mechanism for coexistence occurs in heterogeneous environments where the growth rate increases downstream. This is a common feature in many river systems where nutrient load and/or temperature, which limit primary production upstream, increase downstream. This heterogeneity creates an upstream invasion limit where the invasion wave of a single species is stalled. Since species 2 has its invasion limit upstream of that of species 1, it is able to establish there. Because the weaker competitor (species 2) becomes established further upstream, it has the advantage of a pool of potential colonizers upstream of the dominant competitor (species 1). Downstream of this colonizer pool of species 2, flow removes individuals of both species but delivers only colonizers of species 2. The combined result of these processes is that the competitive superiority of species 1 is lost in some region downstream. Species 1 is not able to persist at its single-species invasion limit but only further downstream at the invasion limit predicted with the competitor at carrying capacity.

This second mechanisms depends on the gradient of the growth rate and is clearly not a boundary effect. It creates spatial areas dominated by only one species and some transition zone in between. Depending on the flow velocity and the steepness of the gradient in growth rate, this coexistence zone can vary in size. Ballyk et al. (1998) modeled resource-mediated competition in a plug-flow reactor and found parameter regimes of spatially mediated coexistence. Whereas the resource in their model is supplied at the top end of the reactor and decreases downstream, we consider the case where the growth rate increases downstream. Cantrell and Cosner (1998) showed how spatially varying growth and interaction rates in a diffusive Lotka–Volterra system can create spatial segregation of competitors and thereby facilitate coexistence. Again, the mechanism here is induced by the advective flow and therefore fundamentally different from the pure diffusive system.

4.3. Spatial scales

Above, we described several possible mechanisms that lead to spatial patterns in population distribution. Our initial investigation was general with respect to the parameter values. Now we explore the spatial scales at which we expect to observe these patterns for realistic parameter values.

Typical growth rates of periphyton (benthic algae) range $0.1-2\,\mathrm{d}^{-1}$ (DeAngelis et al., 1995; Son and Fujino, 2003). Diffusion rates of $0.1-0.5\,\mathrm{m}^2\,\mathrm{s}^{-1}$, and average flow speeds of $0.01-0.03\,\mathrm{m\,s}^{-1}$ were obtained from fitting advection–diffusion equations to data from conservative tracer injection experiments (Bencala and Walters, 1983; Kim et al., 1992). Speirs and Gurney (2001) already concluded for their model that populations cannot persist in a well-mixed water column when individuals are assumed to experience the average flow speed. However, most planktonic or invertebrate species in rivers are not purely pelagic but have benthic stages (Allan, 1995). In that case, the effective flow speed experienced by the population is reduced considerably. First, the flow speed is much reduced near the benthos. According to formula (13) by Speirs and Gurney (2001), the flow speed in the lowest 4% of the river depth is only 10% of the average flow speed. Secondly, relative abundance estimates of benthic and flow populations indicate that for some species individuals spend only as little as 0.01% of the time in the flow (Speirs and Gurney, 2001). When individuals are exposed to the flow only for a fraction of the time, then the effective flow speed that these individuals experience is reduced by the same factor, i.e., by approximately 10^{-4}. Pachepsky et al. (2005) have modeled this transition between benthic and pelagic stages explicitly.

The invasion condition requires that the effective flow speed be bounded by

$$\begin{aligned} V_{\mathrm{eff}} &\leqslant 2\sqrt{DR} \sim 6.8\times 10^{-4} - 6.8\times 10^{-3}\,\mathrm{m\,s}^{-1} \\ &= 0.058 - 0.58\,\mathrm{km\,d}^{-1}. \end{aligned}$$

This requires an effective flow speed that is 10–100 fold lower than the average flow speed of $0.01-0.03\,\mathrm{m\,s}^{-1}$. This reduction clearly falls in the range discussed above.

At first, we turn to the width of the transition zone at the upstream invasion limit for a single species as illustrated in Fig. 1. Setting $D = 0.1\,\mathrm{m}^2\,\mathrm{s}^{-1}$ to its lowest value, we set the growth rate to vary $R = 0.1-0.3\,\mathrm{d}^{-1}$ over a spatial scale of 100 km. An average effective flow speed of $V = 10^{-3}\,\mathrm{m\,s}^{-1}$ puts the invasion limit at $x^* = 58$ km (10). The steady state distribution increases from zero to R over a region of 4 km near the invasion limit. Doubling D and reducing R to half its value leaves the invasion limit unchanged but widens the transition zone to a 6 km region.

Next, we look at the case of boundary coexistence. We fix $D = 0.1\,\mathrm{m}^2\,\mathrm{s}^{-1}$ as above and set $R = 0.2\,\mathrm{d}^{-1}$. The interaction coefficients are as in Section 3. For flow speeds smaller than $2\times 10^{-4}\,\mathrm{m\,s}^{-1}$, species 1 outcompetes species 2. At flow speeds above $7\times 10^{-4}\,\mathrm{m\,s}^{-1}$ species 2 takes over and species 1 goes extinct. In between, both species are present in a range of 5–10 km below the upstream boundary.

Finally, we examine the size of the coexistence region in a heterogeneous habitat. We fix a flow speed of $V = 10^{-3}\,\mathrm{m\,s}^{-1}$. Interaction coefficients are as in Section 3. We set up the diffusion rate and the variation in growth rates over a stream reach of 100 km in such a way that the weaker competitor can invade all the way to the top of the stream and the reduced invasion limit for the superior competitor lies in the 0–100 km region of space. For $D = 0.1\,\mathrm{m}^2\,\mathrm{s}^{-1}$ and a range of $R = 0.3-0.9\,\mathrm{d}^{-1}$ the coexistence zone extends approximately 10 km. Increasing diffusion to $D = 0.3\,\mathrm{m}^2\,\mathrm{s}^{-1}$ while reducing growth to $R = 0.2-0.4\,\mathrm{d}^{-1}$ expands the coexistence region to nearly 20 km. For even higher diffusion of $D = 0.5\,\mathrm{m}^2\,\mathrm{s}^{-1}$ and lower growth $R = 0.1-0.2\,\mathrm{d}^{-1}$, together with increased $\rho = 1.45$ the coexistence region spans almost 50 km.

These examples demonstrate that the mechanisms presented above, and illustrated in Figs. 1–3, can produce patterns on relevant scales of several hundred meters to tens of kilometers. We want to note that the diffusion rates used above only reflect the physical conditions in the flow. We conjecture that biological processes such as grazing and movement by grazers can produce a larger effective diffusion rate, which in turn has the potential to increase the coexistence regions to the order of hundreds of kilometers. Future work will also focus on the effect of the competition coefficients on these patterns.

4.4. Extensions

We chose the Lotka–Volterra equations as the simplest representation of competitive interactions. In reality, these interactions are often mediated though resources, which follow their own dynamics. We recognize the importance of this complexity and plan to incorporate more mechanistic descriptions of competitive processes (e.g. light and nutrient-based algal growth) in future work. Similarly, it will be necessary to compare the results obtained here to models that incorporate more explicit environmental properties of rivers (e.g. hydraulic features (pool-riffle structures), storage zones, spatially explicit nutrient perturbations (point-source versus non-point source inputs)).

Whereas we focused the model and discussion on riverine systems, they may apply to terrestrial systems as well. For example, Potapov and Lewis (2004) use a similar model to study the impact of moving temperature isoclines on competitors. More generally, the coexistence of two or more competitors on a few limiting resources has been and still is a very active field in spatial ecology (Lehmann and Tilman, 1997). The most widely accepted explanation for this paradox is an assumed trade-off between competition and colonization, where frequently colonization ability is related to dispersal ability (Lehmann and Tilman, 1997), for example via seed size (Levin and Muller-Landau, 2000).

In contrast to this, both competitors in our system have exactly the same dispersal ability, indicating that colonization should be thought of as the combination of two processes, namely dispersal ability and growth rate at low density. We conjecture that by allowing the diffusion rates and/or flow speeds to vary between the species, the effects observed above can change in spatial extend, and new effects may appear as in Potapov and Lewis (2004). Diffusion as well as effective flow speed are partly determined by the dynamics of the water (e.g. turbulence, flow) and partly by behavioral factors (e.g. active dispersal, adherence to benthos). Benthic stages have been incorporated into single-species models for river ecosystems (Lutscher et al., 2005; Pachepsky et al., 2005), and it is part of our ongoing research efforts to explore the effects of these stages on competitive systems.

We have concentrated on the spatial mechanisms by which coexistence or competitive reversal can be achieved from a case where the non-spatial model predicts competitive exclusion. We conjecture that the results qualitatively still hold when we replace Lotka–Volterra competition with resource-mediated competition. These models typically predict competitive exclusion as the only outcome in a non-spatial setting (Smith and Waltman, 1995). The non-spatial Lotka–Volterra model also predicts coexistence and founder control in certain regions of parameter space. Future work will assess the effect of diffusion and flow on these outcomes. Neuhauser and Pacala (1999) have shown in a stochastic interacting-particle system that both these regions in parameter space may decrease in size in favor of competitive exclusion when symmetric dispersal is considered. We speculate that in systems with advection, new effects will appear. It may be possible that the ‘‘founder control’’-scenario becomes and ‘‘upstream control’’-scenario, in which the species that invades further upstream dominates the other.

Acknowledgments

The authors thank C. Cosner and H.L. Smith for inspiring discussions. FL gratefully acknowledges support as a PIMS postdoctoral fellow. EM acknowledges support from NSERC and the Canada Research Chair Program. This research was also supported by grants from the NSERC Clean Water Network and the Alberta Ingenuity Centre for Water Research. MAL gratefully acknowledges support from NSERC Discovery and CRO grants and a Canada Research Chair.

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