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Predator–prey systems in streams and rivers

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Abstract Many predator–prey systems are found in environments with a predominantly unidirectional flow such as streams and rivers. Alterations of natural flow regimes (e.g., due to human management or global warming) put biological populations at risk. The aim of this paper is to devise a simple method that links flow speeds (currents) with population retention (persistence) and wash-out (extinction). We consider systems of prey and specialist, as well as generalist, predators, for which we distinguish the following flow speed scenarios: (a) coexistence, (b) persistence of prey only or (c) predators only (provided they are generalists), and (d) extinction of both populations. The method is based on a reaction–advection–diffusion model and traveling wave speed approximations. We show that this approach matches well spread rates observed in numerical simulations. The results from this paper can provide a useful tool in the assessment of instream flow needs, estimating the flow speed necessary for preserving riverine populations.

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Introduction

A large number of organisms live in media that are characterized by a predominantly unidirectional flow. Rivers and streams are particular examples in which the water flow constitutes not only a foundation for the populations living therein, but also provides many beneficial values and services at large (e.g., water supply and groundwater recharge, navigation, nutrient transport and recycling, flood mitigation, and recreational opportunities such as fishing and boating, etc.). Fresh water is a limited and precious resource, and has therefore been in the center of human use and management. Changes in natural flow regimes, however, have put many stream populations at risk. Conflicting interests between water management and ecosystem functioning thus pose a complex dilemma (e.g., Richter et al. 1997), which requires multi-disciplinary solution approaches (Anderson et al. 2006b).

The instream flow need (IFN) is a concept that approaches this problem by trying to identify the magnitude, timing, and variability of flow necessary to preserve desired levels of biodiversity (Poff et al.

1997). Alterations of these flow characteristics can significantly affect the habitat available for populations, as well as their foraging, reproductive, and competitive behavior. For instance, bull trout (*Salvelinus confluentus*) require a habitat that is cold, clean (for spawning and rearing), complex (e.g., streams with riffles and deep pools), and connected (for annual spawning and feeding migrations). Flow alterations could pose significant disturbances, further threatening the bull trout, which are experiencing serious declines in the USA and Canada.

Water withdrawal, as well as river and stream regulations, impact various characteristics of the flow regime, including the current velocity or flow speed. We shall assume that flow alterations, i.e., changes in the discharge or run-off, proportionally affect the flow speed, as discharge and water velocity are linearly related for identical river geometries (e.g., Allan and Castillo 2007; Chaudhry 2008). The question arising is how much the flow can be changed while still maintaining an intact stream ecology. Here we present a simple method to link the flow speed with the persistence or extinction of species within a predator–prey community. The method makes use of invasion speed diagrams and is based on a system of reaction–advection–diffusion equations. There are related mathematical models in the literature, taking into account a single species only, competition, consumption, nonlocal dispersal, spatial heterogeneity, etc. Some of them focus on population persistence as well and/or critical domain sizes (Speirs and Gurney 2001; Pachepsky et al. 2005; Lutscher et al. 2005, 2006, 2007; Byers and Pringle 2006), while others consider characteristic spatial scales, called the response lengths (Anderson et al. 2005, 2006a, 2008; Nisbet et al. 2007). The appeal of the approach presented here is its simple graphical analysis of emerging wave speeds. It readily provides information on the flow needs required for predator–prey populations to persist.

The remainder of this article is organized as follows. The next section introduces the model and its underlying assumptions. The section "Population spread" presents analytical approximations of invasion speeds, upon on which the graphical analysis is based. The section "Results" presents various examples of this analysis for ecologically interesting scenarios. While this section concerns specialist predators, the next one applies the approach to generalist predators. The following section deals with the generality and limitations of the results. The section "Drift-feeding" illustrates, in an example of drift-feeding fish, that water flow can be beneficial. Finally, this article concludes with a discussion and summary of our results.

Model description

We consider populations of prey N and predators P as functions of time t and space x. The environment is assumed to be a well-mixed river or stream that we can approximate by a spatially homogeneous line. The dimensionless model reads

$$N_t = -v N_x + N_{xx} + f(N, P)N , \qquad (1)$$

$$P_t = -\delta v P_x + \varepsilon P_{xx} + g(N, P)P , \qquad (2)$$

where the subscripts denote respective partial derivatives. The advective flow experienced by the prey is denoted by v. We suppose that it is a measure of the actual flow rate of the stream or river under consideration and will henceforth take it as a proxy for this control parameter. The predators may experience different flow speeds than the prey due to behavioral or morphological differences, cf. the section "Different prey and predator flow speeds" for more details. Parameter δ describes the ratio of predator and prey flow speeds. Both prey and predators obey random motion in the form of diffusion. The diffusion coefficient for the prey has been scaled to unity. Parameter ε is the ratio of predator and prey diffusion coefficients. Functions $f(N, P)$ and $g(N, P)$ describe the local per-capita rates of change of prey and predators, respectively, due to growth and interaction. One possible and simple parametrization of these functions is as follows (Volterra 1931):

$$f(N, P) = \alpha(1 - N) - P , \qquad (3)$$

$$g(N, P) = N - \mu . \qquad (4)$$

The prey are assumed to grow logistically in the absence of predators, with intrinsic growth rate α and carrying capacity 1. Consumption of the prey by predators is described, for the sake of simplicity, by a linear functional response of Lotka–Volterra type. Note that the trophic conversion efficiency has been scaled to unity. In the absence of prey, predators decay with a per-capita mortality rate μ. That is, the predators considered here are specialists. The section "Generalist predators" will investigate generalist predators. Details of the non-dimensionalization of the original model can be found in the Appendix A.

To test the analytical approximations we will derive in the next section, we will compare them with results from numerical simulations. Numerical simulations necessarily run on a bounded domain, for which we have to impose boundary conditions. At the upstream end, we assume a dispersal barrier so that no

individuals can leave or enter the river. This is described by zero-flux boundary conditions at $x = 0$:

$$-vN + N_x = 0 \, ,$$

$$-\delta v P + \varepsilon P_x = 0 \, .$$

We assume a long river with the downstream end ($x = L$) being "far" away, i.e., the boundary is supposed to have only little influence. This can be expressed by Danckwert's boundary conditions (cf. Ballyk et al. 1998; Lutscher et al. 2006):

$$N_x = 0 \, , \qquad P_x = 0 \, .$$

We have set $L = 1000$, choosing a river length that is considerably larger than the expected traveling wave front. The simulations have been checked for different step sizes in both time and space.

Population spread

For the following analysis, we assume an unbounded spatial domain, i.e., the length of the river is much larger than the species' dispersal distances, and boundary conditions at the source and outlet can be neglected. As initial conditions, we have the following situation in mind, which is depicted in Fig. 1. There is a nucleus of predators embedded within a nucleus of prey that are placed in an otherwise uninhabited river.

There are two related quantities used to understand the rate of spread of populations. The first is the spreading speed, and the second is the traveling

Fig. 1 Illustration of the initial conditions considered in this paper. The predator population is nested centrally within the prey population, which in turn inhabits a finite domain. Both populations experience a flow in the downstream direction. $c_N \pm v$ and $c_P \pm \delta v$ are the downstream and upstream invasion speeds of prey and predators, respectively (more details in the text)
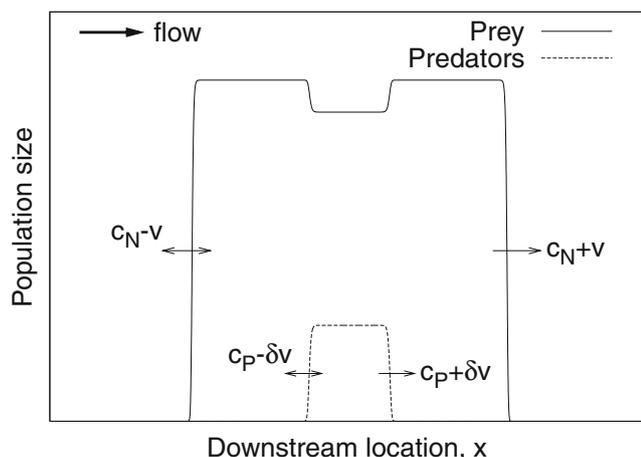
wave speed. The spreading speed is the rate at which a locally introduced population eventually spreads spatially into the surrounding habitat. In a river environment, there will be different upstream and downstream spreading speeds. Traveling wave solutions are special solutions to the partial differential equation model that are translation-invariant, of a fixed shape connecting one steady state (e.g., uninvaded) to another (e.g., invaded), and moving at a constant speed c across the spatial domain. The speed of the traveling wave is typically bounded below by the spreading speed. For example, Fisher's equation (logistic growth with intrinsic growth rate α plus simple diffusion with diffusion coefficient D) has a spreading speed of $c^* = \sqrt{\alpha D}$, and has traveling wave solutions, connecting the zero steady state to the carrying capacity, for all traveling wave speeds $c \geq c^*$ (Aronson and Weinberger 1975). Hence, the spreading speed is the minimum possible traveling wave speed. This is also true for interacting population models where there are cooperative or competitive dynamics (Li et al. 2005), but has not been proved for predator–prey systems.

However, in a system without advection, numerical solutions of the locally introduced predator–prey populations appear to approach the form of traveling waves moving at the minimum possible speed. That is, constant profiles of prey and predator populations asymptotically propagate with a constant speed, which is the minimum traveling wave speed. While noting that there is no proof of the equivalence of minimum traveling wave speed and the spreading speed for predator prey systems, we simply refer to these wave speeds as *reaction–diffusion speeds*. Note that, for the system Eqs. 1–4, without advection, the existence of traveling waves has been mathematically proven by Dunbar (1983, 1984). In a system with advection, we can expect traveling wave fronts in two directions—one downstream with a speed that is increased by the respective flow speed and one upstream that is decreased by the respective flow speed. The down- and upstream speeds therefore have two components that can simply be added or subtracted, namely, the reaction–diffusion speeds plus/minus the respective flow speed (see the Appendix B for details). If c_N and c_P denote the reaction–diffusion speed of the prey and predators, their up- and downstream speeds are

$$c_N \mp v \, , \tag{5}$$

$$c_P \mp \delta v \, . \tag{6}$$

When the flow speed is larger than the reaction–diffusion speed, the upstream speed becomes negative and the direction of the propagating wave is reversed.

This is indicated by the two heads of the arrows in Fig. 1. Negative upstream speeds imply that the population will eventually retreat from the river reach for long times. We will refer to this as *wash-out* by analogy to similar processes in chemostat populations. The downstream speeds are always positive.

The initial conditions chosen will give rise to two invasion scenarios. First, the prey spreads into empty space both up- and downstream. Second, the predators spread into an area up- and downstream that is already occupied by the prey. We will now consider each of these cases separately and determine the wave speeds of prey and predator invasion in upstream and downstream directions.

First, in the absence of predators ($P \equiv 0$), the prey Eq. 1 reduces to

$$N_t = -v N_x + N_{xx} + f(N, 0)N . \tag{7}$$

If $f(N, 0)$ is of logistic type as in Eq. 3, Eq. 7 is the Fisher model (Fisher 1937; Kolmogorov et al. 1937) plus advection. The reaction–diffusion speed of the traveling wave therefore has the minimum speed

$$
\begin{aligned}
c_N &= 2\sqrt{f(0, 0)} \\
&= 2\sqrt{\alpha} \qquad \text{with } f(N, P) \text{ as in Eq. 3.}
\end{aligned} \tag{8}
$$

Second, as for the predator invasion, we can assume that the prey approach the carrying capacity, $N \approx 1$. Then Eq. 2 can be approximated by

$$P_t = -\delta v P_x + \varepsilon P_{xx} + g(1, P)P. \tag{9}$$

Neglecting the advection and for a $g(N, P)$ as in Eq. 4, this gives rise to a minimum speed (cf. Luther 1906; Skellam 1951)

$$
\begin{aligned}
c_P &= 2\sqrt{\varepsilon\, g(1, 0)} \\
&= 2\sqrt{\varepsilon\, (1 - \mu)} \qquad \text{with } g(N, P) \text{ as in Eq. 4,}
\end{aligned} \tag{10}
$$

provided that $0 < \mu < 1$. In the case with high mortality, $\mu > 1$, the predators will always go extinct, cf. Eqs. 3–4. Henceforth, we will restrict our attention to the case $0 < \mu < 1$.

We have obtained wave speed approximations for both invasion scenarios. In the next section, we will compare their values and infer their joint interplay.

Results

As specified by the initial conditions, the prey have some distance from the predators at the beginning

(Fig. 1). In the course of time, the upstream and downstream distances between the prey and predator front change depending on the relative values of the speeds determined in the previous section. We will now identify asymptotic scenarios in which both prey and predators coexist, both go extinct, or only the prey survive.

Consider a fixed flow speed and the invasion of prey and predators into one direction (upstream or downstream). If the prey invasion speed is larger than the predator invasion speed, the distance between them in this direction will increase linearly in time. We will refer to this as *run-away*. In contrast, if the prey spread more slowly than the predators do, the distance between them in this direction shrinks linearly in time until the predator front reaches the prey front. We will refer to this as *catch-up*.

We will now consider these two cases for varying flow speeds and into both upstream and downstream direction. Initially, we assume that prey and predators experience the same flow speed, i.e., $\delta = 1$. In this case, the question if one species is faster than the other reduces to a comparison of the reaction–diffusion speeds, cf. Eqs. 5–6. Later, in the section "Different prey and predator flow speeds," we will relax the assumption of identical flow speeds.

Invasion speed diagram

Figure 2 showcases how upstream and downstream invasion speeds of prey and predators vary with the flow speed v. It is easy to draw this and similar diagrams, which we shall refer to as *invasion speed diagrams*. For vanishing flow speed $v = 0$, there is no difference in upstream and downstream direction. The invasion speeds coincide with the reaction–diffusion speeds, which give the intercepts with the vertical axis. With increasing flow speed, the upstream and downstream invasion speeds diverge linearly with slope ∓ 1 for the prey and slope $\mp \delta$ for the predators (recall that $\delta = 1$ in this example).

Prey run-away

The sample scenario illustrated in Fig. 2 reveals that the prey have a larger reaction–diffusion speed than the predators ($c_N > c_P$). In the downstream direction, the prey are always faster than the predators and, therefore, run away for all flow speeds. In the upstream direction, the prey are always faster as well. However, upstream invasion speeds for both the prey

Fig. 2 Invasion speed diagram for specialist predators that advance more slowly than the prey. The symbols indicate numerically observed spread rates of the respective population in upstream and downstream direction. Equations 1–4 with parameter values $\alpha = 4, \mu = 0.9, \varepsilon = 1, \delta = 1$
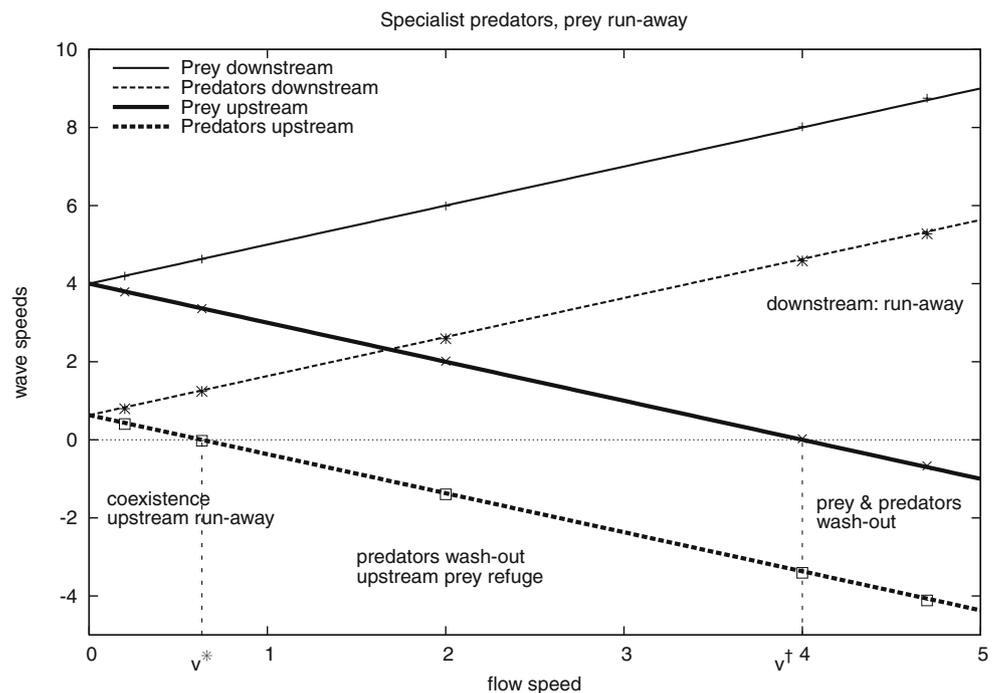
and predators can become negative. This gives rise to different possible outcomes.

(a) If the upstream speeds for prey and predators are positive ($0 \leq v < v^*$), both of them can spread upstream. That is, predators and prey coexist, with the prey running away in the upstream reach. This is illustrated in Fig. 3a.

(b) For $v \approx v^*$, the predator upstream speed is zero. That is, the predator upstream invasion stalls (Fig. 3b). The predators thus maintain a foothold in the river reach, while the prey have an upstream refuge where they are safe from predation. The location of the transition, i.e., the predator foothold, depends on the initial conditions.

(c) For intermediate flow speeds ($v^* < v < v^\dagger$), the predator upstream speed is negative while the prey upstream speed remains positive. The predators get washed-out and, for a long time, will eventually disappear from the entire river reach. The prey are left alone in the habitat without predators, cf. Fig. 3c.

(d) For $v = v^\dagger$, the prey upstream speed becomes zero. This divides the river into an upstream reach without the prey and a downstream reach where the prey are present.

(e) For large flow speeds ($v > v^\dagger$), the prey are also washed out. Both species will asymptotically disappear and go extinct (Fig. 3d).

Obviously, the persistence of a species within the stream is determined by its upstream invasion speed. This is why we shall plot in the following invasion speed diagrams the upstream branches only.

Predator catch-up

If the predator reaction–diffusion speed is larger than the prey reaction–diffusion speed ($c_P > c_N$), there always is a catch-up in both upstream and downstream directions (Fig. 4a). When the predator front reaches the prey front, the wave speed approximations for the predators no longer hold. This is because the prey will not be at the carrying capacity anymore. Rather, we have to consider the situation that both prey and predators spread into empty space simultaneously. Numerical simulations indicate that both species advance with identical speed. In fact, the prey invasion continues with the same speed $c_N \mp v$ as before, while the predator invasion slows down to the prey invasion speed. Taking this into account, the invasion speed diagram in Fig. 4a (illustrating the situation before the catch-up) can therefore be modified to the one in Fig. 4b (illustrating the situation after the catch-up).

We can broadly distinguish the following cases:

(a) If the flow speed is small ($v < v^*$), there is coexistence in both the upstream and downstream reaches. The predators catch up to the prey
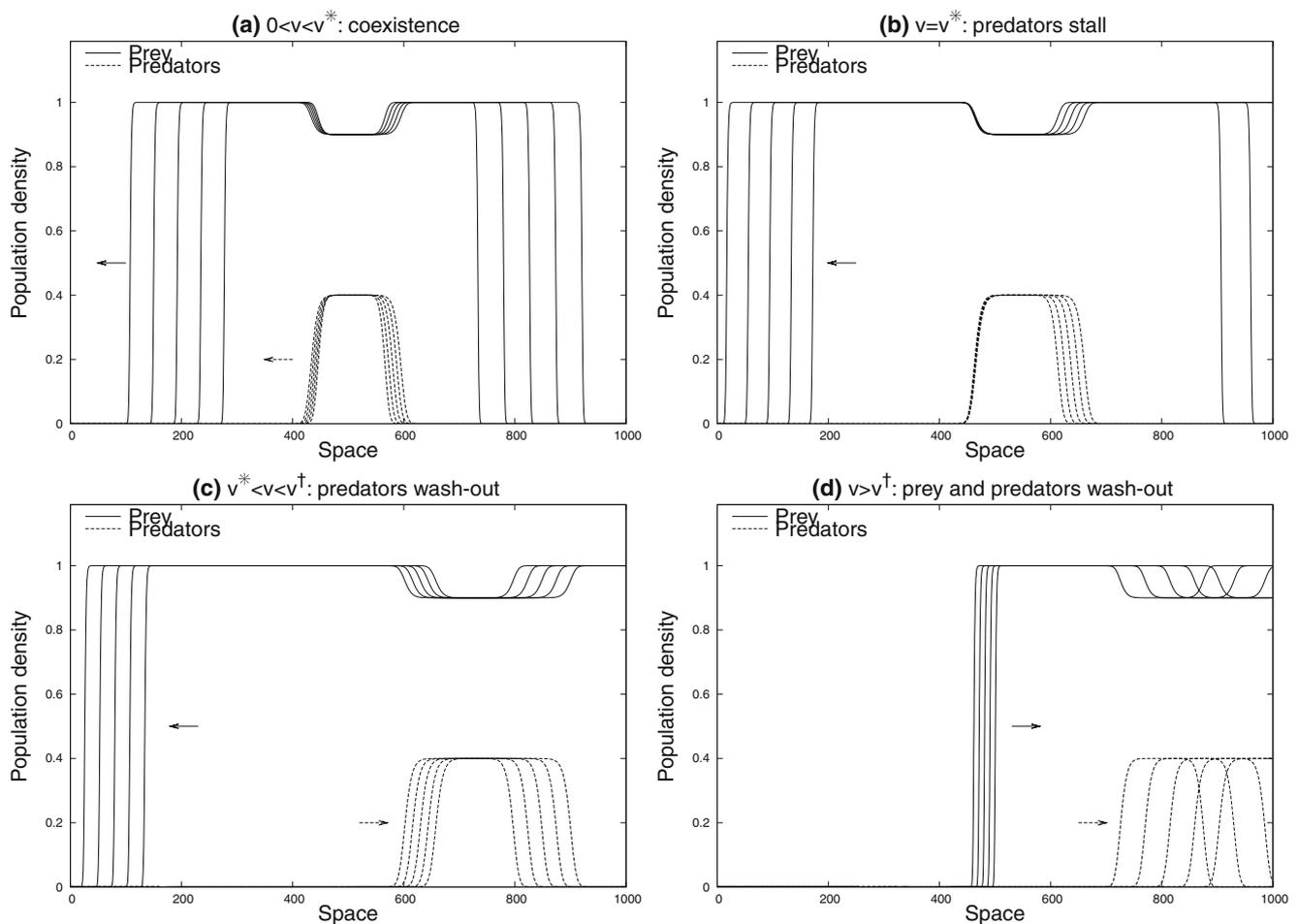
Fig. 3 Illustrations of **a** community coexistence with prey run-away, **b** prey upstream refuge, **c** predators wash-out, and **d** community extinction, depending on river flow speed regimes. The

Eqs. 1–4 with parameter values as in Fig. 2. **a** $v = 0.2$, each ten times units from $t = 30$. **b** $v = 0.632456$, from $t = 60$. **c** $v = 2$, from $t = 100$. **d** $v = 5$, from $t = 60$

invasion fronts and advance in joint fronts with the prey.

(b) For intermediate flow speeds ($v^* < v < v^\dagger$), the prey upstream speed is negative, leading to a wash-out of the prey. Since the predators are specialists, they cannot persist without the prey. Hence, even though the predator upstream invasion speed before catch-up is positive, both prey and predators will be washed out (Fig. 4b). The effective critical flow speed $v^\ddagger$ for prey and predators wash-out coincides with v^*.

(c) For large flow speeds ($v > v^\dagger$), the upstream speeds for both populations are negative, still implying extinction of predators and prey.

Note that, in this scenario (faster predator invasion), the eventual outcome is either coexistence or extinction of both species. There is a unique critical flow speed $v^* = v^\ddagger$ that separates flow regimes allowing coexis-

tence from flow regimes, leading to community extinction. In contrast to the previous scenario (faster prey invasion), there is no regime of flow speeds where the prey can persist without the predators ($v^* < v < v^\dagger$).

Different prey and predator flow speeds

We now consider the case that prey and predators experience different flow speeds, i.e., $\delta \neq 1$. If $\delta > 1$ ($\delta < 1$), the predator flow speed is larger (smaller) than the prey flow speed. This can be caused by a number of mechanisms. For example, the predators could have the capability of directed locomotion and, therefore, increase the effective advective flow speed in pursuit of the prey. Adults of aquatic insects could fly upstream to oviposit, thus balancing the downstream drift (Müller 1954, 1982). Species could also reside mainly on the benthos or have refugia within the river (e.g., Waters 1972; Richardson 1992; Lancaster and Hildrew 1993;

Fig. 4 Invasion speed diagram for specialist predators that advance faster than the prey. **a** Before catch-up and **b** after catch-up. After the catch-up, predators are slowed down to the same spread rate as the prey. This effectively shifts down the predator invasion speed lines and overlays them with the lines for the prey. Equations 1–4 with parameter values $\alpha = 0.2$, $\mu = 0.5$, $\varepsilon = 1$, $\delta = 1$

(a) Specialist predators, before catch-up
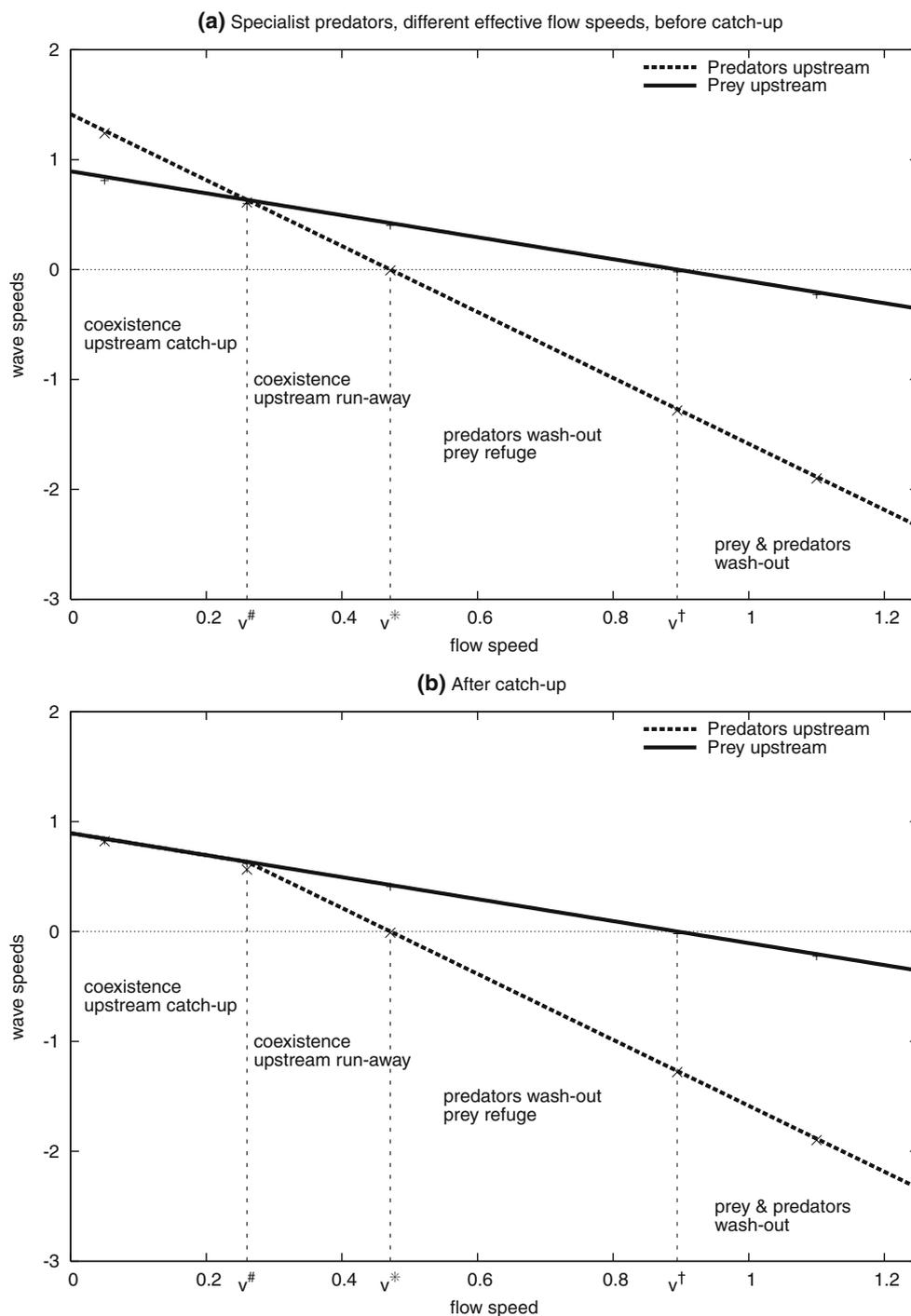

(b) Specialist predators, after catch-up
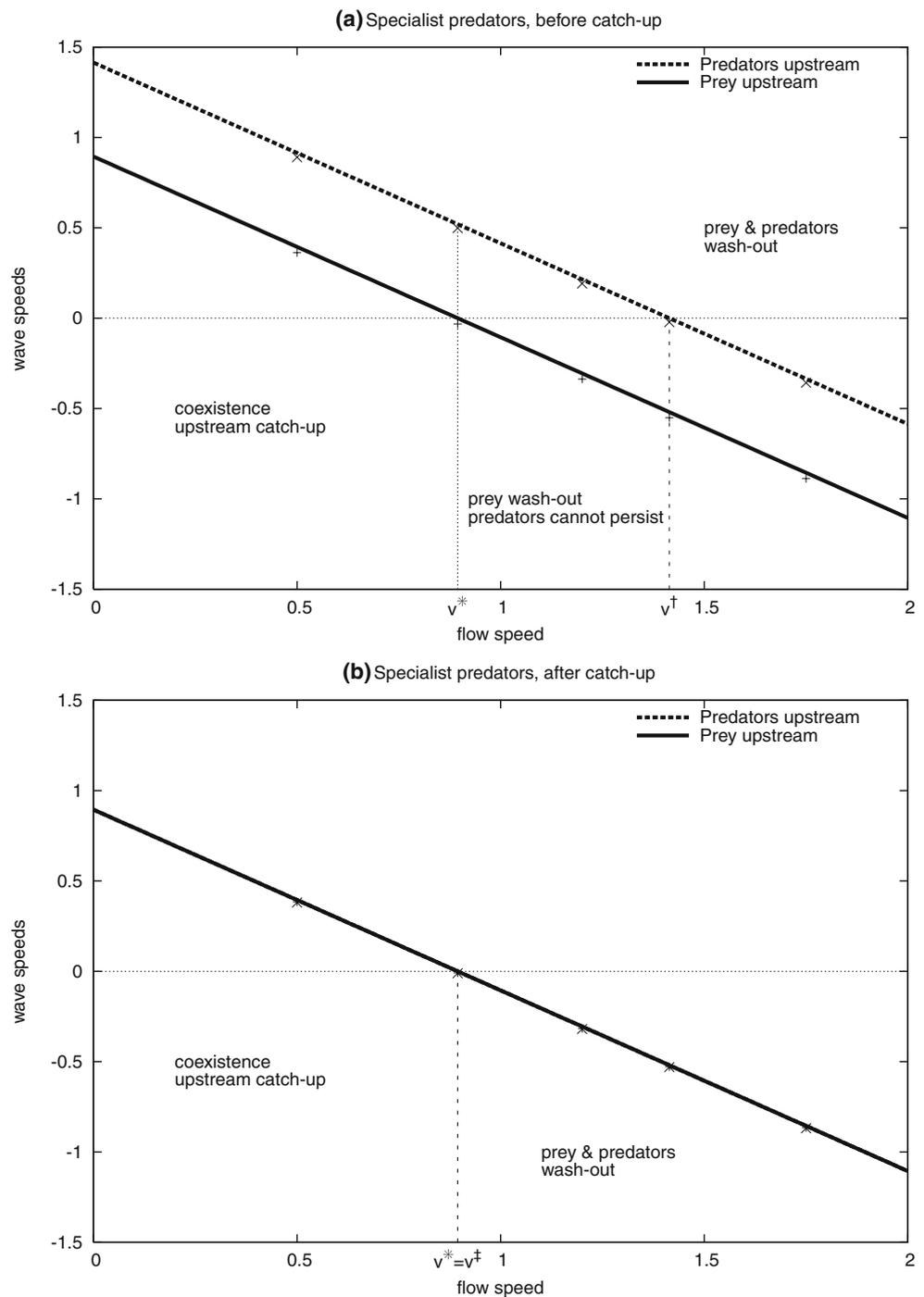
Winterbottom et al. 1997; Rempel et al. 1999; Walks 2007). These mechanisms can effectively increase or decrease the flow speed experienced by a species in comparison with the actual water current. We therefore consider v as the flow speed realized for the prey and δv as the relative flow speed realized by the predators.

If the flow speeds of prey and predators are different, the upstream and downstream speeds of the predators diverge with different slopes ($\delta \neq \mp 1$) than those of the prey (slopes ∓ 1). This is illustrated in Fig. 5. The scenario shown therein assumes that the predators are faster than the prey in the absence of flow and that $\delta > 1$. We can distinguish the following outcomes:

(a)   In the downstream direction and, for small flow speeds ($v < v^{\#}$), in the upstream direction, the predators catch up to the prey (Fig. 5a). Since

Fig. 5 Invasion speed diagram for specialist predators that advance faster than the prey and experience a different flow speed δv. **a** Before catch-up and **b** after catch-up. If it comes to a catch-up, predators are slowed down to the same spread rate as the prey. Equations 1–4 with parameter values $\alpha = 0.2$, $\mu = 0.5$, $\varepsilon = 1$, $\delta = 3$

(a) Specialist predators, different effective flow speeds, before catch-up

(b) After catch-up

the predators are specialists, population spread after catch-up will take place with identical speed, namely that of the prey. Figure 5a can therefore be modified to Fig. 5b.

(b) At $v \approx v^{\#}$, the prey upstream speed becomes larger than the predator upstream speed. From that flow speed on, the prey runs away from the predators in the upstream direction. Hence, in the flow interval $v^{\#} < v < v^{*}$, there is coexistence with a run-away rather than a catch-up.

(c) For flow speeds $v^{*} < v < v^{\dagger}$, the predators get washed-out so that the prey can persist alone.

(d) For large flow speeds ($v > v^{\dagger}$), both species are washed-out.

We saw in the previous subsection ("Predator catch-up") with identical flow speeds that prey with a smaller reaction–diffusion speed ($c_N < c_P$) either co-exist with predators or go extinct. This established a unique critical flow speed $v^* = v^\ddagger$. If the predators experience a larger flow speed ($\delta > 1$), however, the situation changes in that there is another regime of flow speeds ($v^* < v < v^\dagger$) allowing prey persistence without predators.

Conversely, the scenario of predator wash-out and prey survival (for $\delta = 1$, cf. section "Prey run-away") may be changed to the coexistence of both species if $\delta < 1$, i.e., predators experience a smaller flow speed than prey. Obviously, the predators benefit from a decrease in experienced flow speed as they are less likely to be swept away.

Generalist predators

In the previous section, we studied the example of specialist predators that cannot sustain themselves without the prey. In the case of a catch-up, the predators are either slowed down to the prey speed or are washed-out jointly with the prey even when the predator upstream speed is positive. We now consider generalist predators with alternative food sources that can persist in the absence of the prey.

Model description

We assume that the prey Eq. 3 remains unchanged, but that the predator equation can be described with the following per-capita rate of change replacing Eq. 4

$$g(N, P) = \beta(\kappa - P) + N. \tag{11}$$

In the absence of prey, the predators grow logistically to a limit κ and with a maximum per-capita growth rate β. Please see the Appendix A for the original dimensional model. Compared to Eq. 4, the predators now have alternative resources as well as density-dependent limitation in the form of intraspecific competition. This may lead to the situation where the predators drive the prey extinct—an interesting scenario in the context of invasive species causing environmental problems. However, as in the previous section, we henceforth assume that predators and prey are able to coexist. That is, the nontrivial stationary state ($N^* = \frac{\beta(\alpha - \kappa)}{1 + \alpha\beta}$, $P^* = \frac{\alpha(1 + \beta\kappa)}{1 + \alpha\beta}$) is stable. This implies $\alpha > \kappa$, which we shall henceforth consider. Note that, due to the new function Eq. 11, there is an additional stationary state ($N^* = 0$, $P^* = \kappa$) with predators only. It is unstable if $\alpha > \kappa$ and stable otherwise.

Wave speeds

Let us reconsider the catch-up of the prey by the predators. At the leading edge of both the prey and predator fronts, we have $N \approx 0$ and $P \approx 0$. The idea is to approximate both prey and predator invasions again by Fisher waves. In the absence of advective flow and following a similar line of arguments as before, the minimum invasion speed of predators can then be estimated as follows:

$$c_P^{CU} = 2\sqrt{\varepsilon\, g(0, 0)}$$
$$= 2\sqrt{\varepsilon\beta\kappa} \qquad \text{with } g(N, P) \text{ as in Eq. 11.}$$

The superscript refers to the scenario after catch-up. Note that $c_P^{CU} < c_P$, because we assume that the predator growth rate $g(N, P)$ increases with prey abundance. The invasion speed c_N of the prey before catch-up remains unchanged. We can now distinguish two cases, depending on whether the new predator speed after catch-up is still larger or smaller than the prey speed.

1. If $c_P^{CU} > c_N$, the predators advance faster into empty habitat. They will run away from the prey, which we will refer to as *take-over*. The distance between predators and prey increases linearly with time. The prey will have to advance into an area where the predators have grown to their limit κ. This slows down the prey invasion to a minimum speed

$$c_N^{CU} = 2\sqrt{f(0, \kappa)}$$
$$= 2\sqrt{\alpha - \kappa} \qquad \text{with } f(N, P) \text{ as in Eq. 3.} \quad (12)$$

2. If $c_P^{CU} < c_N$, the prey advance faster into empty space. However, they cannot escape from the predators because they follow closely and will catch-up rapidly (recall that $c_P > c_N$). We therefore expect a predator front closely following an invading prey front. This means that the predators are slowed down to the minimum prey speed c_N.
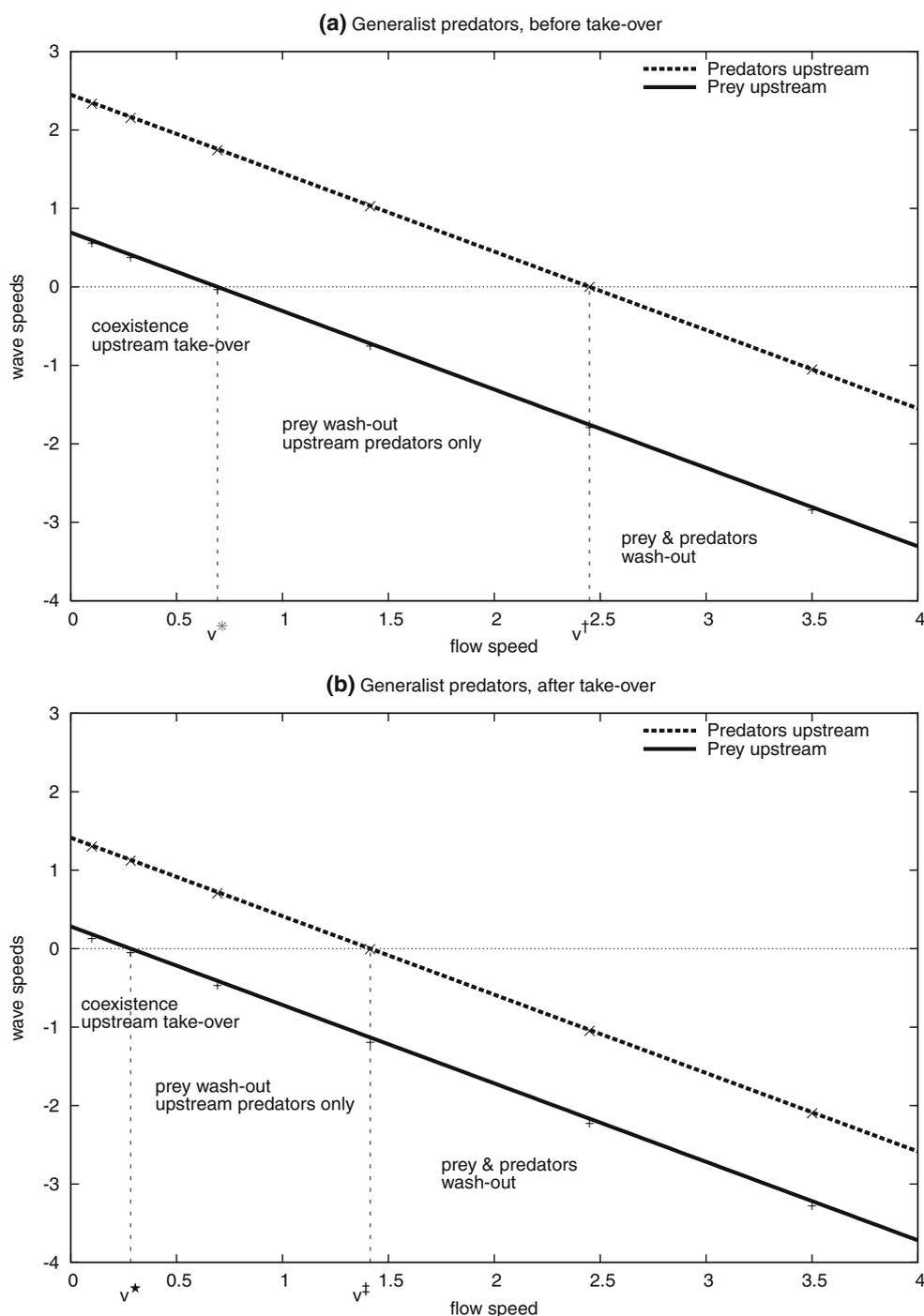
Predator take-over

We now consider the case of a take-over of faster predators, i.e.,

$$c_P > c_P^{CU} > c_N,$$

and identical flow speeds, i.e., $\delta = 1$. Figure 6a shows the upstream and downstream invasion speeds of prey and predators before catch-up. We always expect a take-over, be it because the predators advance faster into open space than the prey or because the prey are

Fig. 6 Invasion speed diagram for generalist predators that advance faster than the prey. **a** Before take-over and **b** after take-over. After take-over, both prey and predator invasion speeds are slowed down, which shrinks the flow regimes facilitating population persistence. Equations 1–3, Eq. 11 with parameter values $\alpha = 0.12, \beta = 5, \kappa = 0.1, \varepsilon = 1, \delta = 1$

(a) Generalist predators, before take-over

(b) Generalist predators, after take-over

washed out for large enough flow speeds. We therefore modify the invasion speed diagram taking into account the speeds after the take-over, i.e., the predators propagate with speed c_P^{CU} and the prey propagate with speed c_N^{CU}. This is shown in Fig. 6b, revealing the following eventual outcomes.

(a) Coexistence of prey and predators is possible for a low flow regime $0 < v < v^\star$.

(b) For intermediate flows ($v^\star < v < v^\ddagger$), the prey are washed out. The predators continue to advance in the upstream direction with the same speed c_P^{CU} that is independent from the prey.

(c) For larger flows ($v > v^\ddagger$), both populations are washed out, leading to extinction of the entire system.

With the predators being generalists, there is a new flow regime ($v^\star < v < v^\ddagger$) not observed before, namely,

prey extinction and persistence of the predators only. In the analogous situation of a specialist predator (Fig. 4), only coexistence or extinction of all species is possible.

It is also interesting to note that the flow regime allowing prey persistence shrinks after take-over, from $v < v^* = 0.69$ in Fig. 6a (before take-over) to $v < v^\star = 0.28$ in Fig. 6b (after take-over). This is because the prey is propagating into habitat occupied by predators, which leads to a reduced prey growth, cf. Eq. 11. Hence, the possibility of coexistence is reduced correspondingly. Moreover, the flow regime allowing predator existence has shrunk as well (from $v < v^\dagger = 2.45$ to $v < v^\ddagger = 1.41$ in Fig. 6). This is because the predators are slowed down after take-over as well. Ahead of the prey front, the predators have only their alternative resources to grow on, but they cannot benefit from the prey anymore. Hence, alternative food sources for the predators allow them to survive without the prey in an intermediate flow regime, but they generally seem to reduce the range of coexistence.

Generality and limitations

Up to now, we have assumed linear predation rates and local growth functions of prey and predators that are of logistic or exponential type. In this section, we will discuss the applicability of invasion speed diagrams to other situations, especially with respect to their practical value. We consider the following generalized model of biomass-conversion type (Section "Drift-feeding" deals with yet another approach specific for drift-feeding stream fish):

$$N_t = -v N_x + N_{xx} + f(N)N - h(N, P)P, \quad (13)$$

$$P_t = -\delta v P_x + \varepsilon P_{xx}$$
$$+ \left[h(N, P) + g_1(P) - g_2(P) \right] P. \quad (14)$$

Function $f(N)$ now represents the per-capita growth rate of prey in the absence of predators. $h(N, P)$ is the functional and numerical response of predators (we still assume that the model has been non-dimensionalized such that the trophic conversion efficiency is equal to one). $g(P) := g_1(P) - g_2(P)$ is the predator per-capita growth rate in the absence of prey. It can be split into a gain term $g_1(P)$ that describes growth by consumption of alternative food and a loss term $g_2(P)$ that describes mortality (e.g., natural deaths or predation by top predators). The predators can be considered specialists if $g(0) \leq 0$ and generalists otherwise.

Table 1 summarizes situations in which the usage of invasion speed diagrams is difficult, limited, or appears to not be possible at all—at least at the current state of knowledge. The reasons behind these complications are discussed in the following subsections. Note that the predator–prey models referred therein have been investigated mostly in a reaction–diffusion context, i.e., without advection.

Allee effects

The Allee effect describes a decline in population growth at small densities, for example, due to difficulties in finding mating partners (e.g. Courchamp et al. 2008). One possible parameterization (cf. Lewis and Kareiva 1993) is

$$f(N) = r(1 - N)(N - u), \quad u \leq 1.$$

With a strong Allee effect ($0 < u < 1$), population growth becomes negative at small densities; in particular, $f(0) < 0$. With a weak Allee effect ($-1 < u \leq 0$), population growth at small densities remains positive, but is reduced. In either case, the maximum per-capita growth rate does not occur at zero population density anymore. This implies that the wave speed

Table 1 Behavior of selected predator–prey models of type Eqs. 13–14 that complicates the practical applicability of invasion speed diagrams, cf. section "Generality and limitations"

$f(N)N$	$g_1(P)P$	$g_2(P)P$	$h(N, P)$	Possible behavior, ref.	Complication
Logistic	–	Linear	Type II	Spatiotemporal chaos [1]	Complex dynamics
Logistic	–	Quadratic	Type II	Bistability [2]	Multistability
Logistic	$g(P)P$ logistic		Type II	Bistability [3]	Multistability
Weak Allee effect	–	Linear	Linear	Predator slow-down [4]	Allee effect
Strong Allee effect	–	Linear	Linear, type II or III	Spread reversal [4]	Allee effect
Strong Allee effect	$g(P)P$ logistic		Type II	Spread reversal [5]	Allee effect
Strong Allee effect	–	Cubic	Linear	Spread reversal [6]	Allee effect
Strong Allee effect	–	Linear	Type II	Patchy invasion [7]	Complex dynamics

References: [1] Sherratt et al. (1995), [2] Steele and Henderson (1981), [3] Magal et al. (2008), [4] Owen and Lewis (2001), [5] Fagan et al. (2002), [6] Petrovskii et al. (2005b), [7] Petrovskii et al. (2002)

approximations would be different (Hadeler and Rothe 1975; Rothe 1981).

The spread of a prey population with a weak Allee effect can be slowed down in the presence of a predator (Owen and Lewis 2001). The spread of a prey population with strong Allee effect can even be reversed (Owen and Lewis 2001); see also Lewis and van den Driessche (1993) and Hilker et al. (2005) for similar retreats of invasion fronts. Such spread reversals mean that the population can go extinct in the absence of any flow, thus making persistence in a stream ecosystem even more difficult.

In principle, the tool of invasion speed diagrams can still be used. The only difference is that the reaction–diffusion speed c_N of the prey may be negative. However, generally speaking, it is more difficult to find an explicit wave speed approximation in a system with Allee effect. Existing approaches include singular perturbation theory (Owen and Lewis 2001) and time scale arguments (Hilker et al. 2005). Exact solutions have been found only for particular models assuming a cubic predator mortality (Petrovskii et al. 2005b).

There is an additional caveat related to strong Allee effects, as they can control the early phase of an invasion. The initial population size as well as the spatial extent need to be large enough to trigger the invasion process at all. Otherwise, the invasion nucleus collapses (Nitzan et al. 1974; Malchow and Schimansky-Geier 1985; Lewis and Kareiva 1993; Kot et al. 1996; Wang et al. 2002; Hilker et al. 2007).

Multistability

A strong Allee effect usually induces bistable dynamics. This means that the population either advances (invades) or retreats (goes extinct). There are a number of ecological mechanisms that can induce bi- or multistability as well. A well-known example is a model system of the spruce budworm, where a static predator with type-III functional response ($h(N, P) = \frac{aN^2}{1+bN^2}$) leads to three nontrivial equilibria, two of which are stable and one of which is unstable (Ludwig et al. 1978). As the trivial equilibrium is unstable as well, one of the two stable equilibria will eventually invade the spatial domain (Murray 2003).

In contrast to the strong Allee effect, such bistability always leads to population spread. The question is just which level of population density is achieved, because one stable equilibrium often corresponds to an "outbreak" state and the other one to a "quiescence" state. This is of interest for biological control, since total eradication is not possible, but the population level can be controlled.

In the context of stream ecosystems, the method of invasion speed diagrams can be used in principle. However, as in the Allee effect case, it is usually more difficult to find approximations of the reaction–diffusion speeds.

A type-III functional response is not the only example of such form of bistability, of course. There are other instances that occur for a type-II functional response ($h(N, P) = \frac{aN}{1+bN}$). A density-dependent predator per-capita mortality ($h_2(P) = -\mu P$) can induce bistability (Steele and Henderson 1981). This kind of mortality is often referred to as quadratic closure of a food chain because it can be used to model the impact of top predators. Hainzl (1988) considers the case $h_2(P) = -\nu - \mu P$. A generalist predator, which can survive with prey and be modeled by $h(P) = \beta(\kappa - P)$, also has an implicit quadratic mortality that can lead to bistability. Strong Allee effect-like bistability is possible as well. The dynamics can be more complicated, including unstable limit cycles and homoclinic loops (Magal et al. 2008).

Complex dynamics

Loosely speaking, we can distinguish two different scenarios with complex spatiotemporal dynamics. The first one typically occurs when the non-spatial system oscillates as in the classical predator–prey model with saturating type-II functional response (Rosenzweig and MacArthur 1963). In the wake of a predator invasion wave, irregular fluctuations appear that correspond to spatiotemporal chaos (Sherratt et al. 1995; Sherratt and Smith 2008). They are self-organized and occur for a wide class of initial conditions (Petrovskii and Malchow 2001; Malchow et al. 2008). Note that spatiotemporal chaos can also be induced by spatial heterogeneity (Pascual 1993).

The second mechanism involves a strong Allee effect in the prey (Petrovskii et al. 2002, 2005a; Malchow et al. 2008) or a subsystem with some kind of bistability (Morozov et al. 2008). Spatial spread does not take place in the form of continuous traveling fronts anymore. Rather, the fronts break up, giving rise to a spread regime called "patchy invasion."

While it is possible to estimate a lower bound for the predator spread rate in the former case ("chaos in the wake of invasion"), see Petrovskii and Malchow (2001), spread rates for the latter case ("patchy invasion") have been investigated only numerically (Morozov et al. 2006). The utility of invasion speed diagrams with respect to their simplicity therefore appears to be restricted to predator–prey communities with a stable coexistence equilibrium—an assumption

also made in Owen and Lewis (2001) and Fagan et al. (2002).

Drift-feeding

In the previous sections, increased flow speed has an exclusively negative effect on population persistence. In fact, all the differential equation-based models we are aware of (cf. references in the introduction) assume that flow tends to wash-out organisms. The purpose of this last section before the final conclusions is to present an example, in which increased flow rate may actually be beneficial for a species, namely, drift-feeding predators.

Many stream fish are drift-feeders, i.e., they hold fixed positions in the water current and feed on

Fig. 7 Invasion speed diagram for drift-feeding predators, **a** before catch-up and **b** after catch-up. The predators' upstream spread rate benefits from increasing water velocity. There is a threshold velocity $v^\S$ that facilitates the emergence of a prey-only scenario at low flow speeds. Parameter values: $\alpha = 4, \mu = 0.9, \varepsilon = d = e = 1$

(a) Drift-feeding predators, before catch-up

(b) Drift-feeding predators, after catch-up
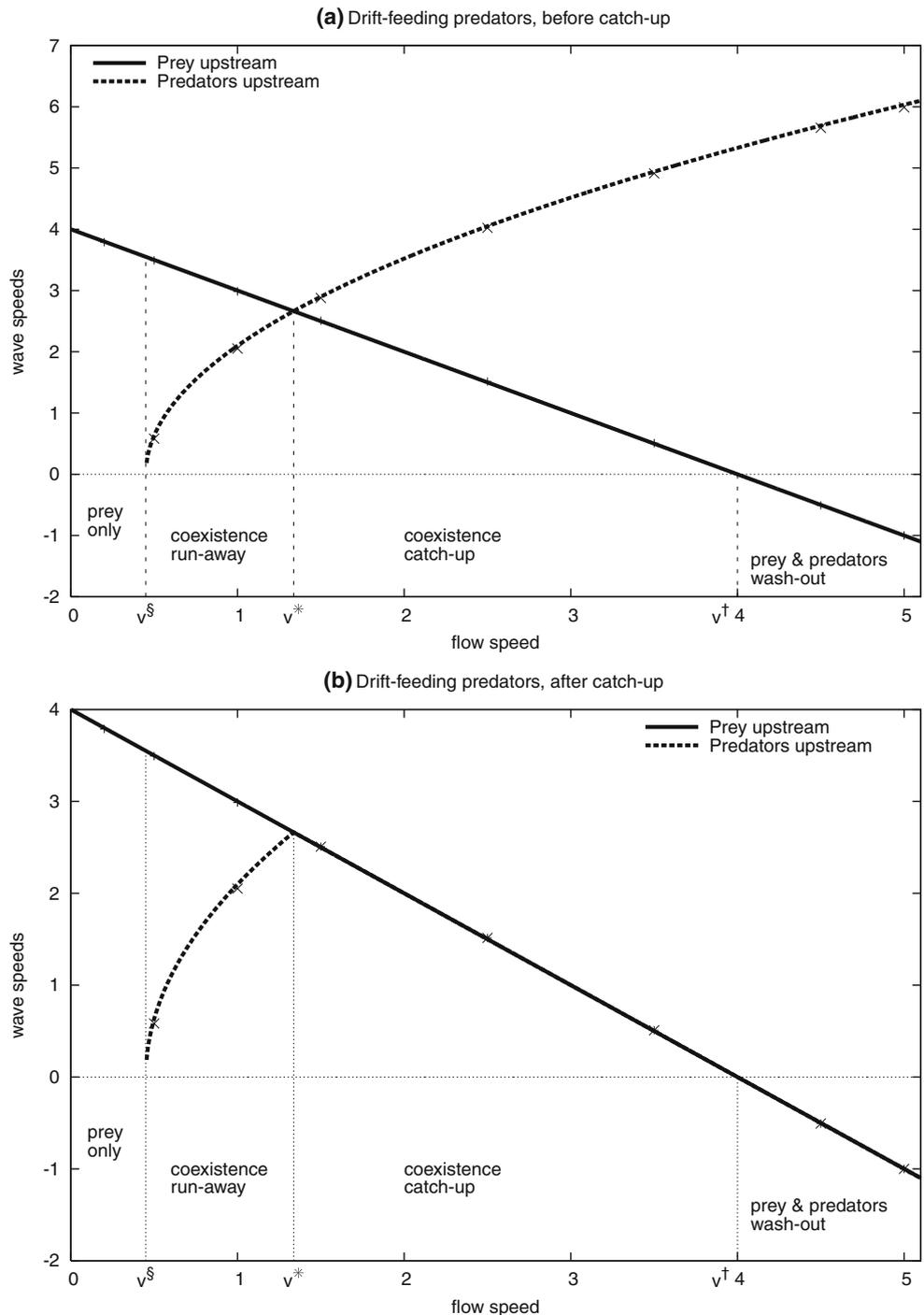
invertebrates that are drifting by. Examples include salmonids such as coho salmon, brook trout, brown trout, steelhead trout, summer chinook, and Arctic grayling. Drift-feeding has received increasing interest due to its importance for stream fish growth and habitat restoration. We now consider a predator–prey model with drift-feeding predators. The novelty is that the functional response also depends on the speed of the water current rather than on the prey population alone.

The rationale behind this is the observation of a proportional relationship between water velocity and drift abundance (e.g., Everest and Chapman 1972; Wańkowski and Thorpe 1979; Fausch 1984; Hughes and Dill 1990; Baker and Coon 1997; Nislow et al. 1999). The amount of prey eaten by a single predator per unit time is assumed to be $2d \times e \times v \times N$, where d is the detection distance of predators per unit time, e is the capture success per prey, and v is the velocity of drifting prey. This approach is similar to an equation for the functional response of a stationary predator to a mobile prey discussed by Holling (1961, p. 167). We further assume that there is no handling time and that the capture success, as well as the detection distance, are constant (but see Hughes and Dill 1990; O'Brien and Showalter 1993; Piccolo et al. 2007). The dynamic equations for the prey and predators, respectively, are

$$N_t = -vN_x + N_{xx} + \alpha(1 - N)N - 2devNP \,, \quad (15)$$

$$P_t = \varepsilon P_{xx} + (2devN - \mu)P \,. \quad (16)$$

Note that there is no advection term for the predators as they are assumed stationary in the current. Utilizing the usual assumption for predator invasion, namely, that the prey $N \approx 1$ reach carrying capacity if predators are initially rare, this gives the following reaction–diffusion speed:

$$c_P = 2\sqrt{\varepsilon(2dev - \mu)}.$$

Hence, in contrast to the previous models, there is a critical flow speed

$$v^\S = \frac{\mu}{2de},$$

below which the predators go extinct and above which they can persist.

Figure 7 illustrates the basic effects of varying water velocity in this drift-feeding model. We assume that $\mu < 2ed\sqrt{\alpha}$; otherwise, there is no intersection of the prey and predator curves because the prey are washed out before the predators are able to persist.

(a) If $v < v^\S$, the predators cannot persist due to a lack of drift. The prey establish in the entire stream at carrying capacity.

(b) For $v^\S < v < v^\ddagger$, predators and prey could coexist, with the prey running away from the predators if $v < v^\star$ and with the predators catching up if $v > v^\star$.

(c) If $v > v^\ddagger$, the prey are washed out and so are their specialist predators.

The following observations are noteworthy:

1. Flow speed has a positive rather than negative effect on the predator population.
2. There is a threshold velocity $v^\S$ necessary for predator emergence.
3. Below this threshold, i.e., for small flow speeds, there is a prey-only scenario, which is another qualitatively new feature of the drift-feeding model.

It should also be noted that species do not drift-feed all the time but pursue other activities. Despite these shortcomings, the model serves to demonstrate that species may benefit from increasing water velocity.

Discussion and conclusions

Increasing and conflicting demands for freshwater resources constitute the need to evaluate IFNs in streams and rivers. If natural flow regimes change (e.g., due to anthropogenic influence), this can directly impact the ecology of organisms inhabiting these habitats. Assessing population and community persistence for varying stream flows therefore is a key issue for biodiversity maintenance in advective environments. We have presented a simple method based on invasion speed diagrams that link different flow speeds to their impact on a population and community level. It can provide useful information on how a population is distributed over space and if a population will persist. These questions are rarely addressed in IFN assessments (Anderson et al. 2006b). Flow speed can be seen as a surrogate for the flow volume (discharge), but there may be situations in which these two quantities are not positively correlated.

We have identified the following possible outcomes that depend on the flow speed, as well as on the population and food web dynamics:

1. Coexistence of prey and predators (for small flow speeds)

2. Extinction of prey and predators (for large flow speeds)
3. Prey-only (for intermediate flow speeds if the prey advances faster than the predators)
4. Predators-only (for intermediate flow speeds if the predators are generalists and advance faster than the prey)

These results appear to suggest that reducing flow speed (e.g., water withdrawal) leads to species coexistence, i.e., improves ecosystem dynamics. This seems to be both counterintuitive and controversial, which is why some remarks of caution and caveats are in order. The standard models considered here rest on the assumption that increased flow speed is generally adverse for organisms by sweeping them away. However, water current can also convey benefits, such as affecting physical factors like water temperature and oxygenation, washing out competitors, and facilitating the transport of resources to the organism or the removal of waste (Allan and Castillo 2007). We have illustrated this, to our knowledge, for the first time in a mathematical model, by the drift-feeding example (section "Drift-feeding"), in which stream fish take advantage of increased drift abundance. These considerations suggest that species coexistence can be reached for intermediate flow speeds, and that there is the possibility of community collapse with loss of the higher trophic levels at low flow speeds as water flows are increasingly diverted for human use.

The invasion speed diagrams remain useful even in these circumstances. They highlight the importance of one crucial quantity that determines the persistence or extinction of a population, namely, the upstream invasion speed. If it is negative, the population will be washed-out and eventually disappear from the river. If it is positive, the population will establish itself and spread in the entire river. If it is identical (or close) to zero, the population will maintain a foothold somewhere in the river. It will establish and spread downstream from the foothold, but it cannot invade (or only very slowly) upstream from this location.

Depending on the invasion speeds of prey and predators, we identified the scenarios of run-away, catch-up, and take-over. In case of a run-away, there will be a river reach where the prey exists without predators. This reach increases with time in spatial length and propagates in both upstream and downstream directions. In case of a take-over, predators can be observed without the prey. And in case of a catch-up, predators and prey will be observed only together.

Alternative resources of generalist predators allow them to coexist without the prey. This facilitates the take-over of the prey front after catch-up. However, without having the prey available, the predators can be substantially slowed down after taker-over. In fact, the flow regime of wash-out becomes more prevalent, and also the prey are negatively affected since they spread into a more hostile habitat with predators. Hence, alternative food is beneficial for the predators in pursuit of the prey, but can be detrimental for the community after catch-up.

The conclusions of this paper are based on asymptotic behavior. In reality, it may take a very long time before the scenarios identified take place, and the populations are likely to be perturbed by other factors that are not considered in our models. For example, spatial heterogeneity is not captured in the well-mixed rivers considered here. The flow speeds could be different in various parts of the rivers (such as riffles and pools), and the population dynamics could vary as well with the quality of different habitats (Lutscher et al. 2006). Also, we have not considered inlets of other streams or rivers that could lead to an external inflow of individuals. Another assumption made is the infinite river length. At locations close to the upstream and downstream ends, boundary effects are likely to occur that will invalidate the analytical invasion speed approximations. The numerical simulations performed, however, indicate an excellent match of analytically approximated minimum wave speeds and spread rates observed on long, but finite, domains.

Many organisms have developed strategies to prevent being washed-out. Stream ecology has long been concerned with the so-called "drift paradox" (Müller 1954, 1974, 1982; Brittain and Eikeland 1988; Allan 1995), i.e., how can a closed population persist while being constantly drifted downstream with extinction appearing inevitable? A number of explanations have been proposed that can resolve this paradox; see the section "Different prey and predator flow speeds" and the references therein. In our model, we have captured some of the mechanisms, including benthic stages and active upstream movement, by taking into account that predators and prey can experience different flow speeds. Both populations also have the potential to move randomly, with identical or different diffusion constants. The diffusive spread of the populations is indeed a prerequisite for population persistence in this model framework (cf. Speirs and Gurney 2001; Humphries and Ruxton 2002).

The discharge and, therefore, the flow regime are subject to some natural variability. This can be due to regular seasonal fluctuations in precipitation and

snowmelt or to more stochastic events such as extreme rainfall or droughts. In fact, for a "healthy" stream, there is usually not just one flow regime. All the hydrological, biological, and geomorphological structures, as well as functions of a riverine system, can only be preserved by intra- and interannual variation in flow. Hence, it is possible that the biological populations temporarily or regularly move from one flow regime to another. That is, a population retreats from a river reach for some time, but then can advance again. This will be further addressed in a separate analysis. It is interesting to note that, in many regions of the world, climate change is expected to increase the temporal variability in flow.

One of the largest merits of the invasion speed diagrams is probably their simplicity. Basically, one needs only two "ingredients." First, the spread rate of a population in an environment without flow, which will give the interception with the vertical axis. This corresponds to the diffusive wave speed, which is determined by the diffusion coefficient and the linearized growth rate at zero densities. There exist various methods to estimate the spread rate from data (e.g., Shigesada and Kawasaki 1997; Turchin 1998). Second, starting from this intercept, one draws two straight lines for the upstream and downstream speeds. The slopes of these lines are given by the flow speed the population experiences. Estimates of this quantity can be obtained as well (for instance, Walks 2007).

The analysis that has been presented here for a predator–prey system is easily applicable also to other multi-species communities, for instance, with competition or infection. Invasion speed diagrams facilitate a straightforward method of estimating the IFN of populations to persist either in isolation or in coexistence with other species. In the presentation of this article, we had particularly riverine environments in mind, although the results can be extended to populations in other advective media. Examples include marine organisms in longshore currents (Gaylord and Gaines 2000; Byers and Pringle 2006), plants or insects in winds with a prevailing direction (Takahashi et al. 2005), species in plug-flow reactors (Ballyk and Smith 1999), and populations facing a pole-wards movement of reference frame due to global warming (Potapov and Lewis 2004).

Appendix A: (Non-)dimensional models

Our starting point is a dimensional model of prey N and predators P at time t and spatial location x:

$$\frac{\partial}{\partial t} N(x, t) = -v_N \frac{\partial}{\partial x} N(x, t) + D_N \frac{\partial^2}{\partial x^2} N(x, t) + f(N, P)N,$$

$$\frac{\partial}{\partial t} P(x, t) = -v_P \frac{\partial}{\partial x} P(x, t) + D_P \frac{\partial^2}{\partial x^2} P(x, t) + g(N, P)P.$$

The downstream advection speeds experienced by the prey and predators are denoted by v_N and v_P, respectively. The diffusivities describing random movement are D_N for the prey and D_P for the predators. The growth function of the prey is given by

$$f(N, P) = r \left(1 - \frac{N}{K} \right) - aP,$$

where r is the intrinsic growth rate, K is the carrying capacity, and a is the predation rate. The growth rates of specialist and generalist predators are differently defined as follows:

A.1 Specialist predators

For specialist predators, we assume

$$g(N, P) = eaN - m,$$

where e is the trophic conversion efficiency and m the mortality rate. Introducing the dimensionless quantities

$$\tilde{N} = \frac{N}{K}, \qquad \tilde{P} = \frac{P}{eK}, \qquad \tilde{t} = eaKt,$$

$$\tilde{x} = \sqrt{\frac{eaK}{D_N}} x, \quad v = \frac{v_N}{\sqrt{eaKD_N}}, \quad \alpha = \frac{r}{eaK},$$

$$\delta = \frac{v_P}{v_N}, \qquad \varepsilon = \frac{D_P}{D_N}, \qquad \mu = \frac{m}{eaK},$$

we arrive at the following dimensionless system:

$$\frac{\partial}{\partial \tilde{t}} \tilde{N} = -v \frac{\partial}{\partial \tilde{x}} \tilde{N} + \frac{\partial^2}{\partial \tilde{x}^2} \tilde{N} + \alpha \tilde{N}(1 - \tilde{N}) - \tilde{N}\tilde{P},$$

$$\frac{\partial}{\partial \tilde{t}} \tilde{P} = -\delta v \frac{\partial}{\partial \tilde{x}} \tilde{P} + \varepsilon \frac{\partial^2}{\partial \tilde{x}^2} \tilde{P} + \tilde{N}\tilde{P} - \mu \tilde{P}.$$

Dropping the tildes for notational convenience gives the dimensionless Eqs. 1–4.

A.2 Generalist predators

For generalist predators, we assume

$$g(N, P) = eaN + b\left(1 - \frac{P}{K_P}\right),$$

where e again is the trophic conversion efficiency. Due to alternative food sources available, the predators grow logistically with intrinsic growth rate b and carrying capacity K_P. Introducing the dimensionless quantities

$$\beta = \frac{b}{aK_P}, \qquad \kappa = \frac{K_P}{eK},$$

we arrive at the following dimensionless system:

$$\frac{\partial}{\partial \tilde{t}}\tilde{N} = -v\frac{\partial}{\partial \tilde{x}}\tilde{N} + \frac{\partial^2}{\partial \tilde{x}^2}\tilde{N} + \alpha\tilde{N}(1 - \tilde{N}) - \tilde{N}\tilde{P},$$

$$\frac{\partial}{\partial \tilde{t}}\tilde{P} = -\delta v\frac{\partial}{\partial \tilde{x}}\tilde{P} + \varepsilon\frac{\partial^2}{\partial \tilde{x}^2}\tilde{P} + \tilde{N}\tilde{P} + \beta\tilde{P}(\kappa - \tilde{P}),$$

where the remaining quantities are defined as in the specialist predators model. Dropping the tildes for notational convenience gives the dimensionless Eqs. 1–3 with Eq. 11.

Appendix B: Derivation of traveling wave speeds

Our first step is to consider traveling wave solutions to system Eqs. 1–2 without the unidirectional flow, i.e.,

$$\frac{\partial}{\partial t}N(x, t) = \frac{\partial^2}{\partial x^2}N(x, t) + f(N, P)N, \quad (17)$$

$$\frac{\partial}{\partial t}P(x, t) = \varepsilon\frac{\partial^2}{\partial x^2}P(x, t) + g(N, P)P. \quad (18)$$

In a second step, we will look at the full system Eqs. 1–2.

Traveling waves are translationally invariant solutions of the form $N(z) = N(x, t)$ and $P(z) = P(x, t)$ with $z = x - ct$. They have a fixed profile and move with constant speed c. Corresponding boundary conditions are

$$N(-\infty) = N_l, \qquad N(+\infty) = N_r,$$

$$P(-\infty) = P_l, \qquad P(+\infty) = P_r.$$

Substituting

$$\frac{\partial}{\partial t}N(x, t) = -cN', \qquad \frac{\partial^2}{\partial x^2}N(x, t) = N'',$$

$$\frac{\partial}{\partial t}P(x, t) = -cP', \qquad \frac{\partial^2}{\partial x^2}P(x, t) = P'',$$

where the primes denote differentiation with respect to z, the partial differential Eqs. 17–18 can be transformed to the following system of ordinary differential equations:

$$-cN' = N'' + f(N, P)N,$$

$$-cP' = \varepsilon P'' + g(N, P)P.$$

Introducing the new variables $O = N'$ and $Q = P'$, we arrive at a system of four differential equations of first order:

$$N' = O, \quad (19)$$

$$O' = -cO - f(N, P)N, \quad (20)$$

$$P' = Q, \quad (21)$$

$$\varepsilon Q' = -cQ - g(N, P)P. \quad (22)$$

Recall that we are interested in two different scenarios (cf. Fig. 1). First, the prey spread into uninhabited space. We can specify the following boundary conditions. For $z \to +\infty$, the prey still need to invade, i.e., $N_r = 0$. For $z \to -\infty$, the prey have already grown to carrying capacity, i.e., $N_l = 1$. Moreover, we can assume that the predators are absent, $P \equiv 0$. Then, system Eqs. 19–22 reduces to

$$N' = O, \quad (23)$$

$$O' = -cO - f(N, 0)N. \quad (24)$$

If $f(N, 0)$ is of logistic type as in Eq. 3, system Eqs. 23–24 corresponds to the Fisher equation (Fisher 1937; Kolmogorov et al. 1937). The minimum wave speed for which traveling wave solutions exist is the one given in Eq. 8. For Fisher's equation, the minimum wave speed corresponds to the spread rate with which a locally introduced population will spread outwards (Aronson and Weinberger 1975).

Second, we are interested in the spread of predators. They propagate into an area where the prey have grown to carrying capacity. Ahead of the wave front, i.e., for $z \to +\infty$, we have $N = 1$ and $P = 0$. Behind the wave front, i.e., for $z \to -\infty$, predators and prey approach their coexistence state (N^*, P^*), cf. Fig. 1. Dunbar (1983, 1984) has proven the existence of such traveling waves and shown that their minimum wave speed is the one given in Eq. 10. This can also be heuristically derived by approximating $N \approx 1$ and $P \approx 0$ at the wave fronts (cf. Shigesada and Kawasaki 1997). System Eqs. 19–22 then reduces to

$$P' = Q, \quad (25)$$

$$\varepsilon Q' = -cQ - g(1, P)P, \quad (26)$$

with $P_l = P^*$ and $P_r = 0$. If $g(1, P)$ is of the type as in Eq. 4, system Eqs. 25–26 corresponds to the Luther/Skellam model (Luther 1906; Skellam 1951). If $g(1, P)$ is of the type as in Eq. 11, system Eqs. 25–26 corresponds to the Fisher model. In either case, the minimum wave speed is given by Eq. 10.

The wave speeds derived here, i.e., Eqs. 8 and 10, are referred to as reaction–diffusion speeds in the main text. Finally, we return to the initial Eqs. 1–2 with advective flow. The advection term is equivalent to using a moving reference frame as in Eqs. 17–18. That is, changing (x, t) to $x - vt$ or $x - \delta vt$ transforms Eqs. 1–2 to the same form as in Eqs. 17–18, cf. Lewis et al. (2009). We just need to consider two types of waves for both prey and predators, depending on whether they spread downstream or upstream. Their respective speeds are given by Eqs. 5 and 6 in the main text.

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