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RESEARCH

# Population Dynamics in River Networks

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**Abstract**
Natural rivers connect to each other to form river networks. The geometric structure of a river network can significantly influence spatial dynamics of populations in the system. We consider a process-oriented model to describe population dynamics in river networks of trees, establish the fundamental theories of the corresponding parabolic problems and elliptic problems, derive the persistence threshold by using the principal eigenvalue of the corresponding eigenvalue problem, and define the net reproductive rate to describe population persistence or extinction. By virtue of numerical simulations, we investigate the effects of hydraulic, physical, and biological factors, especially the structure of the river network, on population persistence.

**Keywords** River network · Population persistence · Eigenvalue problems · Net reproductive rate

**Mathematics Subject Classification** 35K57 · 47A75 · 92D25

## 1 Introduction

River and stream ecosystems form a key component of the global environmental ecosystems, with a characteristic that organisms living in river systems are subjected to

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the biased flow in the downstream direction. Stream ecologists and river managers are interested in the instream flow needs (IFNs) and "drift paradox" problem. The former asks how much stream flow can be changed while still maintaining an intact stream ecology (Anderson et al. 2006; Mckenzie et al. 2012), and the latter asks how stream-dwelling organisms can persist without being washed out when continuously subjected to a unidirectional water flow (Müller 1954, 1982; Pachepsky et al. 2005; Speirs and Gurney 2001). The problems are challenging due to the complex and dynamic nature of interactions between the river environment and the biological community. The study of river population models reveals the dependence of spatial population dynamics on environmental and biological factors in rivers or streams; hence, it has become an important explanation of the IFNs and "drift paradox" problem, see, e.g., Anderson et al. (2006), Lutscher et al. (2006), Mckenzie et al. (2012), Pachepsky et al. (2005), Speirs and Gurney (2001), Jin and Lewis (2011), Lutscher et al. (2005).

In mathematical models for river populations, rivers have been traditionally treated as a bounded or unbounded interval on the real line (see, e.g., Speirs and Gurney 2001; Mckenzie et al. 2012; Jin and Lewis 2011; Lutscher et al. 2005). While spatially and temporally homogeneous river intervals (see, e.g., Speirs and Gurney 2001) are recognized as oversimplification of real river systems, rivers have also been approximated by alternating good and bad patches or pool-and-riffle channels (see, e.g., Lutscher et al. 2006; Jin and Lewis 2014), drift and benthic (or storage) zones (see, e.g., Huang et al. 2016; Pachepsky et al. 2005), or meandering rivers consisting of a main channel and point bars (see, e.g., Jin et al. 2017; Jin and Lewis 2014), etc.

Nevertheless, natural river systems are often in a spatial network structure such as dendritic trees. The network topology (i.e., the topological structure of a network), together with other physical and hydraulic features in a river network, can greatly influence the spatial distribution of the flow profile, including the flow velocity and water depth, in the network. For a population living in a river network, its dispersal vectors may be constrained by the network configuration and the flow profile, and its life history traits may depend on varying habitat conditions in the network. As a result, population distribution and long-term behaviors in river systems can be significantly affected by the network topology or structure, see, e.g., Cuddington and Yodzis (2002), Fagan (2002), Goldberg et al. (2010), Grant et al. (2007), Grant et al. (2010), Peterson et al. (2013). Then there may arise interesting questions such as whether a population can persist in the desert streams of the southwestern USA while the streams are experiencing substantial natural drying trends (Fagan 2002), or whether dendritic geometry enhances dynamic stability of ecological systems or not (Grant et al. 2007). Other related dynamics in the network, such as the dynamics of water-borne infectious diseases like cholera, may also be greatly affected by the river network geometry (see, e.g., Bertuzzo et al. 2010). River networks have been modeled by habitats of discrete patches in individual-based models (Fagan 2002; Grant et al. 2010) and matrix population models for stage-structured populations (Goldberg et al. 2010; Mari et al. 2014). This simplification neglects the spatial heterogeneity within each river branch and can hardly describe the flow effect on the population properly. In recent works (Ramirez 2012; Sarhad and Anderson 2015; Sarhad et al. 2014; Vasilyeva 2019), integro-differential equations and reaction–diffusion–advection (**RDA**) equations were used to model population dynamics in river networks, which were described by continuous graph-like spatial domains, like the networks in the natural world. In their works, a river network was modeled under the framework of a metric graph, which is a graph $G = (V, E)$ with a set $V$ of vertices and a set $E$ of edges, such that each edge is associated with an interval connecting vertices (see, e.g., Berkolaiko and Kuchment 2013); population dynamics in each river branch was modeled by an integro-differential equation or an **RDA** equation on a corresponding edge, and transition conditions were imposed at junction vertices.

The fundamental theories of parabolic and elliptic equations as well as the corresponding eigenvalue problems on metric networks are important in establishing population dynamics of biological species in river networks. The existence and uniqueness of solutions of linear parabolic equations and nonlinear parabolic equations on networks have been established in von Below (1988a, 1994), respectively. A maximum principle for semilinear parabolic equations on networks was obtained in von Below (1991), and the eigenvalue problems associated with parabolic equations on networks were studied in von Below (1988b). Stability of steady states of parabolic equations on networks was studied in von Below and Lubary (2015), Yanagida (2001). More studies of diffusion equations on networks can be found in, e.g., Arendt et al. (2014), Lumer (1980). In these works, the model parameters are allowed to be time and/or space dependent; the so-called Kirchhoff laws or an excitatoric Kirchhoff condition (or dynamical node condition) is assumed at the interior junction vertices. In the current paper we will establish a mathematically rigorous foundation of **RDA** equations in a metric tree, which models population dynamics of a biological species in a river network. The model consists of **RDA** equations describing population dynamics in network branches, conditions of continuous population density and zero population flux at interior junction vertices, and suitable initial conditions and boundary conditions at upstream and downstream vertices, allowing spatial variations of diffusion rates, advection rates, and growth rates throughout the network. We will rigorously derive mathematical theories, such as the maximal principle, the comparison principle, and the existence, uniqueness and estimates of the solutions, for the parabolic equations and the corresponding elliptic equations.

The long-term behavior of a population (e.g., persistence or extinction) has been described by uniform persistence, (in)stability of the trivial solution, existence and stability of positive steady states, the critical domain size (minimal size of the habitat such that a species can persist), etc., see, e.g., Jin and Lewis (2011), Huang et al. (2016), Lam et al. (2016), Lutscher et al. (2005), Mckenzie et al. (2012), Pachepsky et al. (2005). For a single species in one-dimensional rivers, the persistence theory was established in a homogeneous environment in Speirs and Gurney (2001), Lutscher et al. (2005), in temporally varying environments in Jin and Lewis (2011), and in spatially heterogeneous environment in Mckenzie et al. (2012). For a benthic–drift population consisting of individuals drifting in water and individuals staying on the benthos, the critical domain size was studied in a spatially homogeneous river in Pachepsky et al. (2005) and in a river with alternating good and bad channels in Lutscher et al. (2006). In particular, persistence metrics (fundamental niche, source/sink metric, and the net reproductive rate) have been established for a single-stage population in Mckenzie et al. (2012) and for a benthic–drift population in Huang et al. (2016), respectively. Population persistence for a single species in homogeneous river networks has also been studied for integro-differential equations (Ramirez 2012) and for **RDA** equations (Sarhad and Anderson 2015; Sarhad et al. 2014; Vasilyeva 2019), where the flow advection, population dispersal, and growth were assumed to be the same throughout the network and population persistence was determined by the instability of the trivial solution (extinction state). In particular, in Sarhad and Anderson (2015), Sarhad et al. (2014), the principal eigenvalue of the corresponding eigenvalue problem was used to determine the stability of the trivial solution, and most of the analyses and results about persistence conditions were restricted to radial trees, in which all branches of the same order are essentially identical habitats. In Vasilyeva (2019), the persistence condition was derived and proved to guarantee the existence and uniqueness of a positive steady-state solution in a simple $Y$-shaped river network. In our work, we will establish persistence conditions in terms of the principal eigenvalue and the net reproductive rate of a general **RDA** system where the population dispersal and growth, the flow advection, the wetted cross-sectional area, and the length of the branches may vary from branch to branch. We will also prove the existence and uniqueness of a globally attractive positive steady state when the population persists provided that growth rates satisfy certain conditions. The theory of infinite-dimensional dynamical systems and existing theories of parabolic and elliptic equations as well as eigenvalue problems on the real line and on metric networks will be applied. We will also study how different factors influence population persistence and the distribution of the positive steady state (if exists) in the network.

This paper is organized as follows: In Sect. 2, we introduce the notion of the river network of a general tree and the initial boundary value problem for population dynamics in the network. In Sect. 3, we establish the existence of the principal eigenvalue $\lambda^*$ of the corresponding eigenvalue problem and show that if $\lambda^* \leq 0$, then the population will be extinct (the trivial solution is globally asymptotically stable), and that if $\lambda^* > 0$, then the population persists in the sense that there exists a unique positive steady state that is globally attractive. In Sect. 4, we define the next-generation operator and the net reproductive rate $R_0$ and prove that $R_0 = 1$ can be used as a persistence threshold for the population. We also provide a method to calculate $R_0$. In Sect. 5, by virtue of numerical simulations, we study the influences of hydraulic, physical, and biological factors on the net reproductive rate $R_0$ and the positive steady state. In "Appendix A," we provide the derivation of the fundamental theories for the parabolic and elliptic problems on networks, including the maximal principle; the comparison principle; and the existence, uniqueness, and estimates of the solutions.

## 2 Model

### 2.1 The River Network—A Metric Tree

In this work, we assume that the river network is a finite metric tree, i.e., a connected finite metric graph with no cycles, or equivalently, a finite metric graph on which any two vertices can be connected by a unique simple path.

We first introduce the mathematical definition of a river network (a finite tree) and notations on it (see, e.g., von Below 1994). Let $G$ be a $C^\kappa$-network for $\kappa \geq 2$ with the set of vertices

$$E = \{e_i : 1 \leq i \leq N\},$$

the set of edges

$$K = \{k_j : j \in I_{N-1}\}, \quad n \geq 2,$$

and the arc length parameterization $\pi_j \in C^\kappa([0, l_j], \mathbb{R}^2)$ on edge $k_j$, where $N$ and $N-1$ are the numbers of vertices and edges, respectively, and

$$I_{N-1} = \{1, 2, \ldots, N-1\}.$$

The edge $k_j$ is isomorphic to the interval $[0, l_j]$ with length $l_j$ and spatial variable $x_j$ on it, where $x_j = 0$ and $x_j = l_j$ represent the upstream end and the downstream end of $k_j$, respectively. The topological graph $\Lambda = (E, K)$ embedded in $G$ is assumed to be simple and connected. Thus, $\Lambda$ admits the following properties: Each $k_j$ has its endpoints in $E$, any two vertices in $E$ can be connected by a unique simple path with arcs in $K$, and any two distinct edges $k_j$ and $k_h$ intersect at no more than one point in $E$. See Fig. 1 for an example of a river network. Endowed with the above graph topology and metric defined on each edge, $G$ is a connected and compact subset of $\mathbb{R}^2$. The orientation of $G$ is given by the incidence matrix $(d_{ij})_{N\times(N-1)}$ with

$$d_{ij} = \begin{cases} 1 & \text{if } \pi_j(l_j) = e_i \text{ (i.e., } e_i \text{ is the downstream end of the edge } k_j\text{)}, \\ -1 & \text{if } \pi_j(0) = e_i \text{ (i.e., } e_i \text{ is the upstream end of the edge } k_j\text{)}, \\ 0 & \text{otherwise (i.e., } e_i \text{ is not a vertex on the edge } k_j\text{)}. \end{cases} \tag{2.1}$$

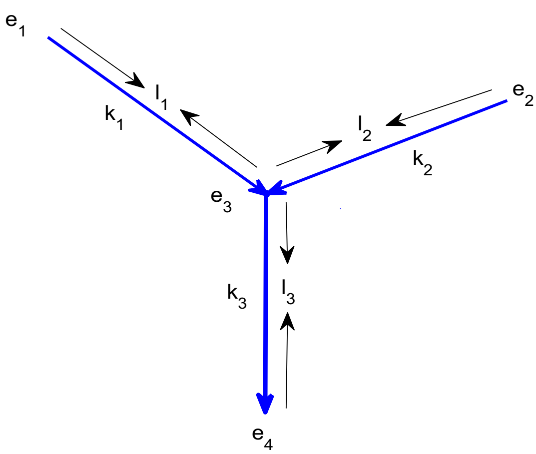



**Fig. 1** An example of a simple river network. Each blue arrow represents a river branch with the specific water flow direction, $l_j$ $(j = 1, 2, 3)$ is the length of the edge $k_j$, and $e_i$ $(i = 1, 2, 3, 4)$ is a vertex

We distinguish the set $E$ of vertices as follows:

$$
\begin{aligned}
E_{\mathrm{r}} &= \{e_i \in E : \gamma_i > 1\} \text{ (ramification (or interior junction) vertices)},\\
E_{\mathrm{b}} &= \{e_i \in E : \gamma_i = 1\} \text{ (boundary vertices)},\\
E_{\mathrm{u}} &= \{e_i \in E : \gamma_i = 1, e_i \text{ is an upstream boundary vertex}\},\\
E_{\mathrm{d}} &= \{e_i \in E : \gamma_i = 1, e_i \text{ is a downstream boundary vertex}\},
\end{aligned}
$$

where $\gamma_i = \gamma(e_i)$ is the valency of $e_i$ that represents the number of edges that connect to $e_i$, and $E_{\mathrm{b}} = E_{\mathrm{u}} \cup E_{\mathrm{d}}$.

Let $t$ be the time variable, and for $T > 0$, denote

$$
\begin{aligned}
&\Omega = G \times [0, T], \quad \Omega_j = [0, l_j] \times [0, T],\\
&\Omega_p = (G \backslash E_{\mathrm{b}}) \times (0, T], \quad \omega_p = (G \times \{0\}) \cup (E_{\mathrm{b}} \times (0, T]).
\end{aligned}
$$

For a function $u : \Omega \to \mathbb{R}$, we define $u_j = u \circ (\pi_j, id) : \Omega_j \to \mathbb{R}$. Differentiation is carried out on each edge $k_j$ with respect to the arc length parameter $x_j$. A function is differentiable on $G$ means that it is differentiable at all points $x \in G\backslash E$. We use the following notations for functions and derivatives at a vertex

$$
\begin{aligned}
&u_j(e_i, t) = u_j(\pi_j^{-1}(e_i), t), \quad u_{x_j}(e_i) = \frac{\partial}{\partial x_j} u_j(\pi_j^{-1}(e_i), t),\\
&u_{x_j x_j}(e_i) = \frac{\partial^2}{\partial x_j^2} u_j(\pi_j^{-1}(e_i), t).
\end{aligned}
$$

Any function $u$ on $\Omega$ satisfies $u_j(e_i, t) = u_h(e_i, t)$ if $k_j \cap k_h = \{e_i\}$.

We now introduce function spaces on $G$. Let

$$
C(G) = \{g : g_j \in C([0, l_j], \mathbb{R}),\ j \in I_{N-1}\}
$$

with the norm:

$$
\|g\|_{C(G)} = \max_{j \in I_{N-1}} \max_{x \in [0, l_j]} |g_j(x)|.
$$

The Banach space $C^m(G)$ consists of all functions that are $m$ times continuously differentiable over $G$ with norm given by

$$
\|g\|_{C^m(G)} = \sum_{\beta=1}^{m} \|g^{(\beta)}\|_{C(G)} + \|g\|_{C(G)},
$$

where $g^{(\beta)}$ is the $\beta$th derivative of $g$. Similarly, $L^p(G)$ is the Banach space of all real-valued functions defined on $G$ that are measurable and $p$-summable with respect to $G$ with $p \geq 1$. The norm in this space is defined by

$$\|g\|_{L^p(G)} = \sum_{j=1}^{N-1} \Big( \int_0^{l_j} |g_j|^p \Big)^{1/p}.$$

For $\alpha \in [0, 1)$, define

$$C^{2+\alpha,1+\frac{\alpha}{2}}(\Omega) = \Big\{ u \in C(\Omega) : \;\; u_j \in C^{2+\alpha,1+\frac{\alpha}{2}}(\Omega_j), \;\; \forall j \in I_{N-1} \Big\},$$

where $C^{2+\alpha,1+\frac{\alpha}{2}}(\Omega_j)$ with the usual norm $\|\cdot\|_{C^{2+\alpha,1+\frac{\alpha}{2}}(\Omega_j)}$ denotes the Banach space of functions $u$ on $\Omega_j$ having continuous derivatives $\frac{\partial^{r+s} u}{\partial t^r \partial x_j^s}$ for $2r + s \le 2$ and finite Hölder constraints of the indicated exponents in the case of $\alpha > 0$. Then $C^{2+\alpha,1+\frac{\alpha}{2}}(\Omega)$ is a Banach space endowed with the norm

$$\|u\|_{C^{2+\alpha,1+\frac{\alpha}{2}}(\Omega)} = \sum_{j=1}^{N-1} \|u_j\|_{C^{2+\alpha,1+\frac{\alpha}{2}}(\Omega_j)}.$$

Similarly, we can define $C^{2+\alpha}(G)$, $W_p^2(G)$, and $W_p^{2,1}(\Omega)$ for any fixed $\alpha \in [0, 1)$ and $p \ge 1$.

### 2.2 The Population Model in the River Network

Since Speirs and Gurney's work (Speirs and Gurney 2001), the dynamics of a population living in a one-dimensional river has been described by the following reaction–diffusion–advection equation:

$$\frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} - v \frac{\partial u}{\partial x} + f(x, u)u, \tag{2.2}$$

where $u(x, t)$ is the population density at location $x$ and time $t$, $D$ is the diffusion coefficient, $v$ is the flow velocity, and $f$ is the per capita growth rate.

We adapt model (2.2) to a population living in a river network $G$. The dynamics of the population can be described by

$$\frac{\partial u_j}{\partial t} = D_j \frac{\partial^2 u_j}{\partial x_j^2} - v_j \frac{\partial u_j}{\partial x_j} + f_j(x_j, u_j)u_j, \;\; x_j \in (0, l_j), \;\; j \in I_{N-1}, \;\; t > 0, \tag{2.3}$$

where $u_j$ is the population density on the edge $k_j$, $D_j$ is the diffusion coefficient on $k_j$, $v_j$ is the flow velocity on $k_j$, and $f_j$ is the per capita growth rate on $k_j$. The initial population distribution in $G$ is denoted by $u^0$, that is,

$$u_j(x_j, 0) = u_j^0(x_j), \; x_j \in [0, l_j], \;\; j \in I_{N-1}. \tag{2.4}$$

There are three types of vertices in the river network $G$: upstream boundary ends, downstream boundary ends, and interior junction vertices. Correspondingly, boundary or interface conditions are imposed at each vertex of $E$.

- At an upstream boundary point $e_i \in E_\mathrm{u}$ that only connects to edge $k_j$, the boundary condition can be assumed as

$$\alpha_{j,1} u_j(e_i, t) - \beta_{j,1} \frac{\partial u_j}{\partial x_j}(e_i, t) = 0 \ \text{ with } \alpha_{j,1} \geq 0,\ \beta_{j,1} \geq 0,\ \alpha_{j,1} + \beta_{j,1} > 0, \tag{2.5}$$

for instance,

$$\text{the zero-flux boundary condition:} \quad \left( D_j \frac{\partial u_j}{\partial x_j} - v_j u_j \right)(e_i, t) = 0. \tag{2.6}$$

- At a downstream boundary point $e_i \in E_\mathrm{d}$ that only connects to edge $k_j$, the boundary condition can be assumed as

$$\alpha_{j,2} u_j(e_i, t) + \beta_{j,2} \frac{\partial u_j}{\partial x_j}(e_i, t) = 0 \ \text{ with } \alpha_{j,2} \geq 0,\ \beta_{j,2} \geq 0,\ \alpha_{j,2} + \beta_{j,2} > 0, \tag{2.7}$$

for instance,

$$\text{the free flow (or Neumann) condition:} \quad \frac{\partial u_j}{\partial x_j}(e_i, t) = 0 \ \text{ or} \tag{2.8}$$

$$\text{the hostile (or Dirichlet) condition:} \quad u_j(e_i, t) = 0. \tag{2.9}$$

- At an interior junction point $e_i \in E_\mathrm{r}$, the population density is continuous and the total population flux in and out is zero. Hence, the continuity conditions and Kirchhoff laws hold at $e_i$:

$$u_{i_1}(e_i, t) = u_{i_2}(e_i, t) = \cdots = u_{i_m}(e_i, t), \tag{2.10a}$$

$$\sum_{j=i_1}^{i_m} d_{ij} A_j D_j \frac{\partial u_j}{\partial x_j}(e_i, t) = 0, \tag{2.10b}$$

where $e_i \in E_\mathrm{r}$ connects to edges $k_{i_1}$, $k_{i_2}$, ..., and $k_{i_m}$, $d_{ij}$ is defined in (2.1), $A_j$ is the wetted cross-sectional area of the edge $k_j$, and (2.10b) is the result of substituting the continuity condition (2.10a) and the condition of flow conservation at $e_i$

$$\sum_{j=i_1}^{i_m} d_{ij} A_j v_j = 0, \tag{2.11}$$

into the condition of zero population flux at $e_i$

$$\sum_{j=i_1}^{i_m} d_{ij} A_j \left( D_j \frac{\partial u_j}{\partial x_j} - v_j u_j \right)(e_i, t) = 0. \tag{2.12}$$

According to different ecological conditions at boundary vertices on $G$, we further use the following notations throughout the paper:

$$E_0 = \{e_i \in E_\mathrm{b} : \text{ vertices with hostile (or Dirichlet) condition}\},$$
$$E_\mathrm{b} \backslash E_0 : \text{ vertices not assigned with hostile condition.}$$

We finally define an initial boundary value problem for a population in a river network:

$$\textbf{(IBVP)} \qquad (2.3),\ (2.4),\ (2.5),\ (2.7),\ \text{ and } (2.10).$$

Furthermore, we impose the following assumptions in different parts of the paper.

**[H1]** For each $j \in I_{N-1}$, $D_j > 0$, $v_j \geq 0$, $A_j > 0$.
**[H2]** For each $j \in I_{N-1}$, $f_j : [0, l_j] \times [0, \infty) \to \mathbb{R}$ is continuous and there exists a constant $M_j > 0$ such that $f_j(x, u) \leq 0$ for any $x \in [0, l_j]$ and $u \geq M_j$, and $f_j(\cdot, u_j)u_j$ is Lipschitz continuous in $u_j$ with Lipschitz constant $L_j > 0$.
**[H3]** For each $j \in I_{N-1}$, $f_j(\cdot, u_j)$ is strictly monotonically decreasing in $u_j$.

By adapting theories for parabolic and elliptic equations on intervals and/or networks (Mugnolo 2012; Arendt et al. 2014; Fijavž et al. 2007; Protter and Weinberger 1967; von Below 1988a, 1991, 1994; Ladyzenskaja et al. 1968; Solonnikov 1965; Pao 1992; Ye et al. 2011), we develop the fundamental theories of parabolic and elliptic problems on networks corresponding to **(IBVP)**, see "Appendix A." In particular, for linear parabolic problems, we establish the strong maximum principle (in Lemma A.1); Hopf boundary lemma for networks (in Lemma A.2); comparison principle (in Lemma A.3); and the existence, uniqueness, and $L^p$ and Schauder estimates of solutions (in Theorem A.4, via writing the differential operator into a self-adjoint operator on the network); for the nonlinear problem **(IBVP)**, we develop the theory of the existence, uniqueness, and positivity of solutions (in Theorem A.7, by using the method of upper and lower solutions) and prove the monotonicity and strict subhomogeneity of the solution map (in Lemmas A.8 and A.9, respectively); for the corresponding elliptic problems, we also obtain the strong maximum principle (in Lemma A.10); Hopf boundary lemma (in Lemma A.11); comparison principle (in Lemma A.12); and the existence, uniqueness, and $L^p$ and Schauder estimates of solutions (in Theorems A.13 and A.15). These mathematical preparations enable us to establish the persistence/extinction criteria for system **(IBVP)**.

## 3 The Eigenvalue Problem and Population Persistence

In this section, we consider the eigenvalue problem associated with the linearized system of **(IBVP)** at the trivial solution, establish the existence of the principal eigenvalue, and then use the principal eigenvalue as a threshold to determine population persistence and extinction. We also obtain the existence, uniqueness, and attractivity of a positive steady state when the population persists. Assumptions **[H1]–[H3]** are imposed in the rest of the paper.

### 3.1 The Eigenvalue Problem and Its Principal Eigenvalue

We first introduce some Banach spaces which will be used frequently later. Denote

$$X = \{\varphi \in C^1(G): \ \varphi \text{ satisfies } (2.5) \text{ and } (2.7)\}, \tag{3.1}$$

and let

$$X_+ = \{\varphi \in X: \ \varphi \geq 0\} \tag{3.2}$$

be the positive cone in $X$. The interior of $X_+$ is

$$X^o = \{\varphi \in X: \ \varphi > 0 \text{ on } G\backslash E_0, \text{ and } d_{ij}\varphi_{x_j}(e_i) < 0 \text{ if } e_i \in E_0\}. \tag{3.3}$$

Then $X_+$ is a solid cone of $X$ with non-empty interior $X^o$. We also write $\varphi_1 \gg \varphi_2$ if $\varphi_1 - \varphi_2 \in X^o$.

The linearization of **(IBVP)** at the trivial solution $u = 0$ is

$$\begin{cases} \dfrac{\partial u_j}{\partial t} = D_j \dfrac{\partial^2 u_j}{\partial x_j^2} - v_j \dfrac{\partial u_j}{\partial x_j} + f_j(x_j, 0)u_j, \quad x_j \in (0, l_j), \ j \in I_{N-1}, \ t > 0, \\ (2.4), \ (2.5), \ (2.7), \ \text{ and } (2.10). \end{cases} \tag{3.4}$$

Substituting $u_j(x_j, t) = e^{\lambda t}\psi_j(x_j)$ into (3.4), we obtain the corresponding eigenvalue problem

$$\begin{cases} \lambda\psi_j(x_j) = D_j \dfrac{\partial^2 \psi_j}{\partial x_j^2} - v_j \dfrac{\partial \psi_j}{\partial x_j} + f_j(x_j, 0)\psi_j, & x_j \in (0, l_j), \ j \in I_{N-1}, \\ \alpha_{j,1}\psi_j(e_i) - \beta_{j,1}\dfrac{\partial \psi_j}{\partial x_j}(e_i) = 0, & \forall e_i \in E_{\mathrm{u}}, \\ \alpha_{j,2}\psi_j(e_i) + \beta_{j,2}\dfrac{\partial \psi_j}{\partial x_j}(e_i) = 0, & \forall e_i \in E_{\mathrm{d}}, \\ \psi_{i_1}(e_i) = \cdots = \psi_{i_m}(e_i), \ \sum_{j=i_1}^{i_m} d_{ij}A_j D_j \dfrac{\partial \psi_j}{\partial x_j}(e_i) = 0, & \forall e_i \in E_{\mathrm{r}}. \end{cases} \tag{3.5}$$

For simplicity, denote $\mathcal{L}$ to be the operator such that $\mathcal{L}|_{k_j} = \mathcal{L}_j$, where

$$\mathcal{L}_j = D_j \frac{\partial^2}{\partial x_j^2} - v_j \frac{\partial}{\partial x_j} + f_j(\cdot, 0). \tag{3.6}$$

The following result indicates that (3.5) admits a simple eigenvalue $\lambda^*$ associated with a positive eigenfunction $\psi^* \in X^o$. We call $\lambda^*$ the *principal eigenvalue* of (3.5). The proof of the proposition is given in "Appendix B."

**Proposition 3.1** *The eigenvalue problem* (3.5) *admits a simple eigenvalue $\lambda^*$ associated with a positive eigenfunction $\psi^* \in X^o$. None of the other eigenvalues of* (3.5) *corresponds to a positive eigenfunction, and if $\lambda \neq \lambda^*$ is an eigenvalue of* (3.5)*, then* $\mathrm{Re}(\lambda) \leq \lambda^*$.

We say that $\mathcal{L}$ has the *strong maximum principle property* if $u \in C^2(G)$ satisfying

$$\begin{cases} -\mathcal{L}_j u_j(x_j) \geq 0, & x_j \in (0, l_j),\ j \in I_{N-1}, \\ \alpha_{j,1} u_j(e_i) - \beta_{j,1} \dfrac{\partial u_j}{\partial x_j}(e_i) \geq 0, & \forall e_i \in E_{\mathrm{u}}, \\ \alpha_{j,2} u_j(e_i) + \beta_{j,2} \dfrac{\partial u_j}{\partial x_j}(e_i) \geq 0, & \forall e_i \in E_{\mathrm{d}}, \\ u_{i_1}(e_i) = \cdots = u_{i_m}(e_i),\ \sum_{j=i_1}^{i_m} d_{ij} A_j D_j \dfrac{\partial u_j}{\partial x_j}(e_i) \geq 0, & \forall e_i \in E_{\mathrm{r}} \end{cases} \tag{3.7}$$

implies that $u > 0$ in $G \backslash E_0$ unless $u \equiv 0$. We also say that $u \in C^2(G)$ is an upper solution of $\mathcal{L}$ if (3.7) holds, and $u$ is called a strict upper solution of $\mathcal{L}$ if it is an upper solution but is not a solution. Then the analysis of Du (2006), Theorem 2.4) can be easily adapted to conclude the following result.

**Proposition 3.2** *The following statements are equivalent.*

(i) *$\mathcal{L}$ has the strong maximum principle property;*
(ii) *$\mathcal{L}$ has a strict upper solution which is positive in $G \backslash E_0$;*
(iii) $\lambda^* < 0$.

### 3.2 Population Persistence or Extinction

A positive steady state of **(IBVP)** satisfies the following elliptic problem:

$$\begin{cases} -D_j \dfrac{\partial^2 u_j}{\partial x_j^2} + v_j \dfrac{\partial u_j}{\partial x_j} = f_j(x_j, u_j) u_j, & x_j \in (0, l_j),\ j \in I_{N-1}, \\ \alpha_{j,1} u_j(e_i) - \beta_{j,1} \dfrac{\partial u_j}{\partial x_j}(e_i) = 0, & \forall e_i \in E_{\mathrm{u}}, \\ \alpha_{j,2} u_j(e_i) + \beta_{j,2} \dfrac{\partial u_j}{\partial x_j}(e_i) = 0, & \forall e_i \in E_{\mathrm{d}}, \\ u_{i_1}(e_i) = \cdots = u_{i_m}(e_i),\ \sum_{j=i_1}^{i_m} d_{ij} A_j D_j \dfrac{\partial u_j}{\partial x_j}(e_i) = 0, & \forall e_i \in E_{\mathrm{r}}. \end{cases} \tag{3.8}$$

The following result shows how the sign of $\lambda^*$ affects the stability of the trivial solution as well as the existence and attractivity of a positive steady state for **(IBVP)**. The proof is given in "Appendix C."

**Theorem 3.3** *Let $\lambda^*$ be the principal eigenvalue of the eigenvalue problem* (3.5).

(i) *If $\lambda^* \leq 0$, then $u \equiv 0$ is globally attractive for* **(IBVP)** *for all initial values in $X_+$.*
(ii) *If $\lambda^* > 0$, then* **(IBVP)** *admits a unique positive steady state $u^* \in X^o$ which is globally attractive for all initial values in $X_+ \backslash \{0\}$.*

Theorem 3.3 indicates that $\lambda^*$ is the key quantity to determine persistence or extinction for a population living in a river network. The population persists if $\lambda^* > 0$, and the population will become extinct if $\lambda^* \leq 0$.

# 4 The Net Reproductive Rate $\mathcal{R}_0$

The net reproductive rate has been defined and proved to be a threshold quantity for population persistence in a single river channel (Mckenzie et al. 2012; Huang et al. 2016). In this section, we will define the next-generation operator and the net reproductive rate $\mathcal{R}_0$ for **(IBVP)** and then use $\mathcal{R}_0$ to determine population persistence and extinction. Moreover, we will provide a numerical method to calculate $\mathcal{R}_0$.

## 4.1 Definition of the Net Reproductive Rate $\mathcal{R}_0$

Assume that the growth rate of the population on edge $k_j$ satisfies $f_j(x_j, u_j)u_j = \tilde{f}_j(x_j, u_j)u_j - m_j(x_j)u_j$, where $\tilde{f}_j$ is the recruitment rate and $m_j(x_j)$ is the mortality rate. Let $r_j(x_j) = \tilde{f}_j(x_j, 0)$, and assume $r, m \in C(G)$. Then

$$\frac{\partial(f_j(\cdot, u_j)u_j)}{\partial u_j}(x_j, 0) = f_j(x_j, 0) = r_j(x_j) - m_j(x_j).$$

For $\phi^0 \in X$, assume that $\phi$ satisfies

$$\begin{cases} \dfrac{\partial \phi_j}{\partial t} = D_j \dfrac{\partial^2 \phi_j}{\partial x_j^2} - v_j \dfrac{\partial \phi_j}{\partial x_j} - m_j(x_j)\phi_j, & x_j \in (0, l_j),\ j \in I_{N-1},\ t > 0, \\ \phi_j(x_j, 0) = \phi_j^0(x_j), & x_j \in [0, l_j], \\ \phi \text{ satisfies (2.5), (2.7), and (2.10).} & \end{cases} \tag{4.1}$$

Define $\Gamma : X \to X$ by

$$[\Gamma(\phi^0)]_j(x_j) = \int_0^\infty r_j(x_j)\phi_j(x_j, t)\mathrm{d}t,\ \ x_j \in [0, l_j],\ \ j \in I_{N-1},$$

where $\phi$ is the solution of (4.1) with initial condition $\phi^0$. That is, $\Gamma$ is a linear operator mapping an initial distribution of the population to its offspring distribution. Hence, we call $\Gamma$ the *next-generation operator*. Let

$$\mathcal{R}_0 = r(\Gamma),$$

where $r(\Gamma)$ is the spectral radius of $\Gamma$ on $X$. Then $\mathcal{R}_0$ represents the average number of offsprings that an individual produces during its lifetime, and we call $\mathcal{R}_0$ the *net reproductive rate*.

Let $B : \mathcal{D} \to \mathcal{D}$ with

$$\mathcal{D} = \{\varphi \in C^2(G \backslash E_b) \cap C^1(G) : \ \ \varphi \text{ satisfies (2.5), (2.7), (2.10)}\} \tag{4.2}$$

be defined by

$$B_j = D_j \frac{\partial^2}{\partial x_j^2} - v_j \frac{\partial}{\partial x_j} - m_j(x_j), \ \ j \in I_{N-1}.$$

Let $\Gamma_1 : X \to X$ be such that

$$[\Gamma_1(\phi^0)]_j(x_j) = \int_0^\infty \phi_j(x_j, t)\mathrm{d}t, \ \ x_j \in [0, l_j], \ \ j \in I_{N-1},$$

where $\phi$ is the solution of (4.1). Similarly as in Proposition 2.10 of Mckenzie et al. (2012), we can prove that $-\Gamma_1$ is the inverse operator of $B$, i.e., $B^{-1} = -\Gamma_1$. Hence, $\Gamma(\phi) = -QB^{-1}(\phi)$, where the operator $Q$ is defined as

$$[Q(\phi)]_j(x_j) = r_j(x_j)\phi_j(x_j), \ \ \forall x_j \in [0, l_j], \ \ j \in I_{N-1}, \forall \phi \in X.$$

Then $\mathcal{L} = B + Q$. By Proposition 3.1 and the above analysis, noting that $(\lambda I - B)^{-1}$ is defined such that

$$[(\lambda I - B)^{-1}(\phi^0)]_j(x_j) = \int_0^\infty e^{-\lambda t}\phi_j(x_j, t)\mathrm{d}t, \ \ x_j \in [0, l_j], \ \ j \in I_{N-1},$$

where $\phi$ is the solution of (4.1), we know that both $\mathcal{L}$ and $B$ are resolvent-positive operators in $X$. It follows from Propositions 3.1 and 3.2 that the spectral bound $s(B)$ of $B$ is the principal eigenvalue of $B$ and $s(B) < 0$. We then obtain the following result by using Thieme (2009), Theorem 3.5.

**Lemma 4.1** *$\mathcal{R}_0 - 1$ and $\lambda^*$ have the same sign, where $\lambda^*$ is the principal eigenvalue of the eigenvalue problem (3.5).*

Theorem 3.3 and Lemma 4.1 imply the following result.

**Corollary 4.2** *If $\mathcal{R}_0 \leq 1$, then $u \equiv 0$ is globally attractive for* **(IBVP)***; if $\mathcal{R}_0 > 1$, then* **(IBVP)** *admits a unique positive steady state $u^* \in X^o$, which is globally attractive for all initial values in $X_+ \backslash \{0\}$.*

Therefore, $\mathcal{R}_0 = 1$ is the threshold for population persistence and extinction. The population will be extinct if $\mathcal{R}_0 \leq 1$, and it will persist if $\mathcal{R}_0 > 1$.

### 4.2 Calculation of $\mathcal{R}_0$

Let

$$\overline{B}_j = D_j \frac{\partial^2}{\partial x_j^2} - v_j \frac{\partial}{\partial x_j}, \ \ j \in I_{N-1}.$$

Integrating (4.1) with respect to $t$ from 0 to $\infty$ yields

$$\int_0^\infty \frac{\partial \phi_j}{\partial t}\mathrm{d}t = \int_0^\infty \left[ D_j \frac{\partial^2 \phi_j}{\partial x_j^2} - v_j \frac{\partial \phi_j}{\partial x_j} - m_j(x_j)\phi_j \right] \mathrm{d}t,\ j \in I_{N-1}.$$

Note that $\phi_j(\cdot, t) \to 0$ as $t \to \infty$. The above equation implies that

$$\begin{cases} -\phi_j^0(x_j) = \overline{B}_j[(\Gamma_1(\phi^0))_j] - m_j(x_j)(\Gamma_1(\phi^0))_j], & j \in I_{N-1}, \\ \Gamma_1(\phi^0) \text{ satisfies (2.5), (2.7), and (2.10).} \end{cases} \tag{4.3}$$

Therefore, $\Gamma_1(\phi^0)$ is the solution of

$$\begin{cases} -\phi_j^0(x_j) = \overline{B}_j u_j(x_j) - m_j(x_j)u_j(x_j), & x_j \in (0, l_j),\ j \in I_{N-1}, \\ u \text{ satisfies (2.5), (2.7), and (2.10).} \end{cases} \tag{4.4}$$

We define

$$T_1 : X \to X,\ u = T_1\phi^0,$$

where $u$ is the solution of (4.4). Then $T_1$ is a compact and strongly positive operator on $X$. By the definition of $T_1$ and equations (4.3) and (4.4), we know that $\Gamma_1 = T_1$ on $X$. Hence, $\Gamma = Q\Gamma_1$ is also a compact and strongly positive operator on $X$. It follows from Du (2006), Theorem 1.2 that $\mathcal{R}_0 = r(\Gamma) > 0$ is a simple eigenvalue of $\Gamma$ with an eigenfunction $\phi^* \in X^o$, i.e.,

$$\Gamma\phi^* = \mathcal{R}_0\phi^*,$$

and there is no other eigenvalues of $\Gamma$ associated with positive eigenfunctions.

By following the idea in the proof of Wang and Zhao (2012), Theorem 3.2, we can obtain $\mathcal{R}_0$ via the principal eigenvalue of another eigenvalue problem.

**Theorem 4.3** *If the eigenvalue problem*

$$\begin{cases} \mu r_j(x_j)\varphi_j(x_j) = -D_j \dfrac{\partial^2 \varphi_j}{\partial x_j^2} + v_j \dfrac{\partial \varphi_j}{\partial x_j} + m_j(x_j)\varphi_j, & x_j \in (0, l_j),\ j \in I_{N-1}, \\ \alpha_{j,1}\varphi_j(e_i) - \beta_{j,1}\dfrac{\partial \varphi_j}{\partial x_j}(e_i) = 0, & \forall e_i \in E_{\mathrm{u}}, \\ \alpha_{j,2}\varphi_j(e_i) + \beta_{j,2}\dfrac{\partial \varphi_j}{\partial x_j}(e_i) = 0, & \forall e_i \in E_{\mathrm{d}}, \\ \varphi_{i_1}(e_i) = \cdots = \varphi_{i_m}(e_i),\ \ \displaystyle\sum_{j=i_1}^{i_m} d_{ij}A_jD_j\frac{\partial \varphi_j}{\partial x_j}(e_i) = 0, & \forall e_i \in E_{\mathrm{r}}, \end{cases} \tag{4.5}$$

*admits a unique positive eigenvalue $\mu^0$ with a positive eigenfunction, then $\mathcal{R}_0 = 1/\mu^0$.*

To numerically calculate $\mathcal{R}_0$, we use the finite difference method to discretize (4.5) and approximate (4.5) by

$$\mu\hat{r}\varphi = \hat{A}\varphi,$$

where $\hat{r}$ is a diagonal matrix containing values of $r(x_j)$ on the main diagonal and $\hat{A}$ is the discretization of the operator on the right-hand side of (4.5). The matrix $\hat{A}^{-1}\hat{r}$ is a nonnegative and irreducible matrix. The Perron–Frobenius theorem implies that $\hat{A}^{-1}\hat{r}$ admits a simple principal eigenvalue $\varsigma^*$, which is the unique eigenvalue of $\hat{A}^{-1}\hat{r}$ that is associated with a positive eigenvector $\varphi^*$, that is,

$$\hat{A}^{-1}\hat{r}\varphi^* = \varsigma^*\varphi^*. \tag{4.6}$$

Then we approximate $1/\mu^0$ by $\varsigma^*$, i.e.,

$$\mathcal{R}_0 = \frac{1}{\mu^0} \approx \varsigma^* \tag{4.7}$$

by using Theorem 4.3 and above approximating scheme.

Note that the next-generation operator $\Gamma$ can be approximated by $\hat{r}\hat{A}^{-1}$. This implies that the eigenvalue problem $\Gamma\phi^* = \mathcal{R}_0\phi^*$ can be approximated by $\hat{r}\hat{A}^{-1}\phi^* \approx \varsigma^*\phi^*$. It follows from (4.6) that $\hat{r}\varphi^*$ is a positive eigenvector of $\hat{r}\hat{A}^{-1}$ corresponding to $\varsigma^*$, i.e., $\hat{r}\hat{A}^{-1}(\hat{r}\varphi^*) = \varsigma^*(\hat{r}\varphi^*)$. Thus, $\hat{r}\varphi^*$ can be used to approximate the eigenfunction $\phi^*$ of $\Gamma$ associated with the eigenvalue $\mathcal{R}_0$. We call $\phi^*$ (or $\hat{r}\varphi^*$ as approximation) the *next-generation distribution* of the population.

## 5 Numerical Simulations

The results in Sects. 3 and 4 show that both the principal eigenvalue $\lambda^*$ of the eigenvalue problem (3.5) and the net reproductive rate $\mathcal{R}_0$ can be used to determine population persistence or extinction. For the biological significance of $\mathcal{R}_0$, now we apply the theory in Sect. 4 to investigate the influences of biotic and abiotic factors on the population's long-term behavior of **(IBVP)** via numerical studies of $\mathcal{R}_0$ and the positive steady state (if exists).

Real river networks are complex, and the quantitative influence of a factor on population persistence highly depends on the structure and scales of the network. While the choice of a general river network is random, we consider a few simple but typical river networks of trees with one, three, four, five, and seven branches, representing different types of network topologies, merging from the upstream or splitting into the downstream, see Fig. 2. In particular, river networks (1), (3-a), (3-b), (7-a), and (7-b) are radial trees, which are rooted trees with all tree features, including edge lengths, cross-sectional areas, and boundary conditions depending only on the distance to the root (see Sarhad et al. 2014).

Three sets of boundary conditions for **(IBVP)** are considered (see, e.g., Mckenzie et al. 2012; Sarhad and Anderson 2015):

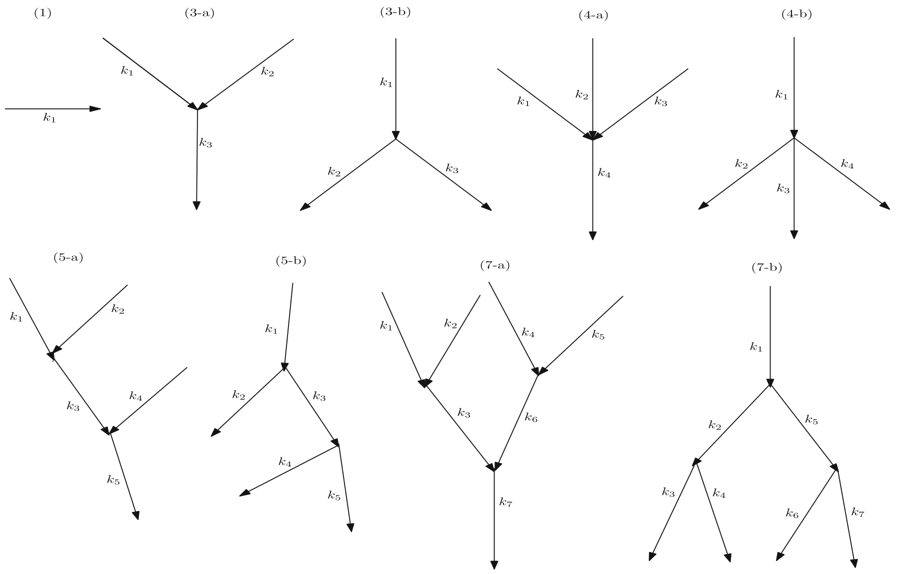



**Fig. 2** River networks that are considered in **(IBVP)** in Sect. 5. The arrows represent the direction of the water flow. The $i$th branch of the network is represented by $k_i$

- (ZF-FF): Zero-flux condition (2.6) at the upstream end and free flow (i.e., Neumann) condition (2.8) at the downstream end—organisms do not cross the upstream boundary but can freely leave the downstream boundary;
- (ZF-H): Zero-flux condition (2.6) at the upstream end and hostile condition (2.9) at the downstream end—organisms do not cross the upstream boundary and they die (or are removed) at the downstream boundary;
- (H-H): Hostile condition (2.9) at both the upstream and the downstream ends—organisms die (or are removed) at the upstream and downstream boundaries.

We adopt the baseline parameters in Speirs and Gurney (2001) for **(IBVP)**. All parameters and their unites are given in Table 1. Note that for simplicity, we choose a constant growth rate $r_j$ on each edge $k_j$, which may result in discontinuity of the growth rate $r(x)$ at interior vertices of the network but should not change the essence of the results as it can be considered as an approximation of a continuous growth function in the network.

**Table 1** Parameters for **(IBVP)** and their units

| Parameter | $L$ and $l_j$ | $D_j$ | $v_j$ | $A_j$ | $r_j$ | $m_j$ | $Q_j$ | $n_j$ | $B_j$ | $S_{0j}$ | $y_j$ |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Unit | m | $m^2/s$ | m/s | $m^2$ | 1/s | 1/s | $m^3/s$ | $s/m^{1/3}$ | m | m/m | m |

### 5.1 The Influence of the River Network Structure on Population Persistence

Natural rivers are rarely in the form of single branches but in various types of networks. The structure (or topology) of a river network influences hydrodynamics as well as the dynamics of ecosystems in the network. To see how the network structure influences population persistence, we compare the values of the net reproductive rate $\mathcal{R}_0$ in all the river networks in Fig. 2. For simplicity, we assume constant growth rate and diffusion rate throughout each network, but allow for varying habitat conditions in the simulations in this subsection.

#### 5.1.1 The Influence of the Total Length of the Network on $R_0$

For a specific type of network structure, variations of the length of branches yield larger (longer) or smaller (shorter) river systems. One may easily ask such a question as whether a population grows better in a small river system or a large river system. On the other hand, one may also wonder whether a simple river shape or a complex river structure is more beneficial to a population given that the total length of the river is the same.

We assume that each network in Fig. 2 is of equal branch lengths (i.e., $l_j$ is constant within a network), and vary the total network length ($L = \sum l_j$) to see how population dynamics changes with the total length $L$ in each network. Figure 3 shows that, under the three sets of boundary conditions, when the total length of the network increases, the net reproductive rate $\mathcal{R}_0$ increases in all the networks. This coincides with the well-known result in one-dimensional river (see, e.g., Jin and Lewis 2011; Lutscher et al. 2005): Given the same habitat conditions, increasing the total habitat size helps population persistence.

Note that network (1) is a radial tree of order 1, that networks (3-a) and (3-b) are radial trees of order 2, and that networks (7-a) and (7-b) are radial trees of order 3. In a radial tree, population dynamics in the branches of the same order (e.g., $k_1$ and $k_2$ in network (3-a)) is identical. Figure 3 also shows that when the total network length $L$ is the same, the $R_0$ in network (1) is larger than the one in networks (3-a) and (3-b), that the $R_0$ in network (3-a) is larger than the one in network (7-a), and that the $R_0$ in network (3-b) is larger than the one in network (7-b). This indicates that in a radial tree, if the total length of the network is fixed, then increasing the number of orders only reduces the value of $\mathcal{R}_0$ and does not help the population to persist. However, one cannot conclude a general result from this that, when the total river length is fixed, the networks with more branches admit smaller net reproductive rates. In the non-radial networks (4-a,b) and (5-a,b), the values of $R_0$ in networks (5-a) and (5-b) may be larger than those in networks (4-a) and (4-b), see Fig. 3a, c, e, f.

We actually consider two cases of flow conditions in Fig. 3. (1) The advection rates ($v_j$'s) are the same throughout the network (e.g., for the sake of ecological protection), and the cross-sectional areas in different branches ($A_j$'s) vary according to the flow conservation relation at interior junctions (2.11), see Fig. 3a, c, e. (2) The cross-sectional areas are the same in the network (e.g., for specific construction requirement), and the flow advection rates vary according to (2.11), see Fig. 3b, d, f. By comparing the left panels and the right panels in Fig. 3, we also find that in the

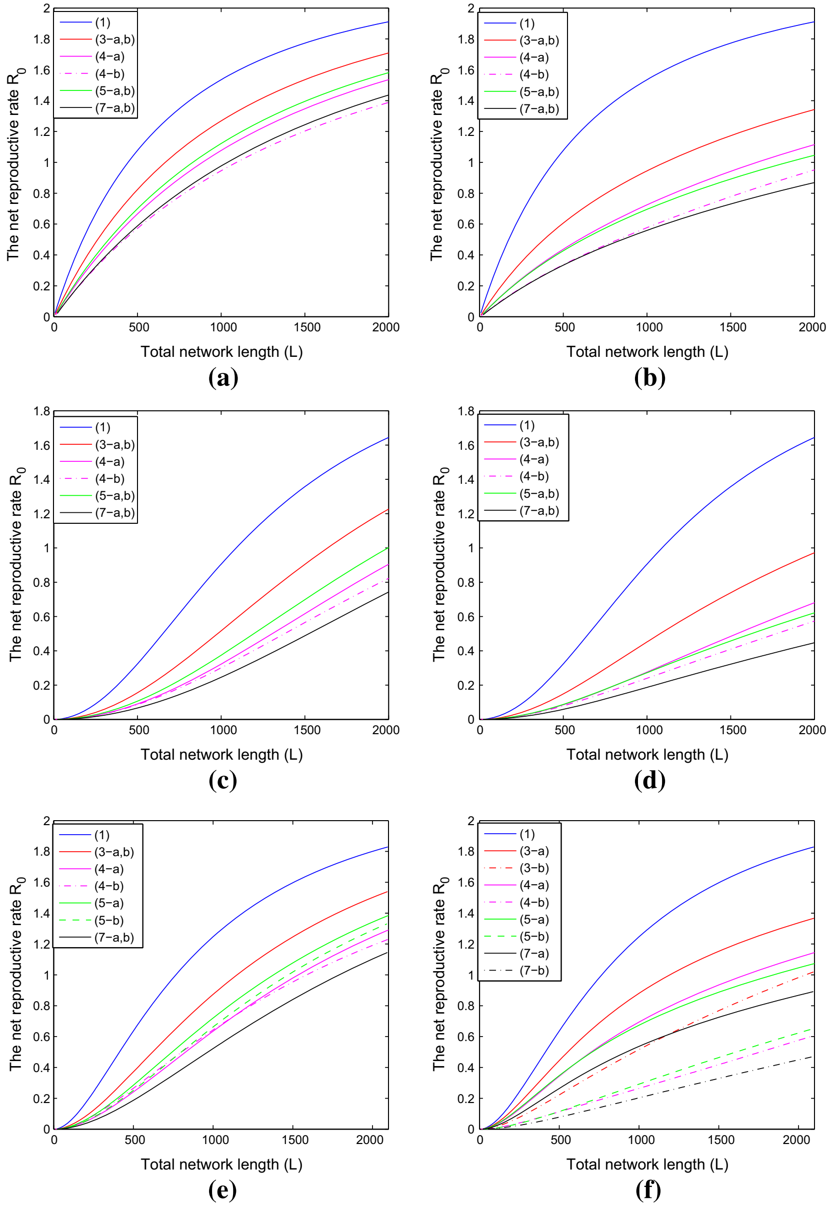



**Fig. 3** The relationship between $\mathcal{R}_0$ and the total length $L$ of the river network. The curve "(*)" represents $\mathcal{R}_0$ in network (*) in Figure 2. Parameters: $D_j = 0.35$, $m_j = 0.0000007$, $r_j = 0.0000052$. In **a**, **c**, **e**, the flow advection rate is the same in the network $v_j = 0.0015$; the cross-sectional area is $A_j = 1$ in the most upstream branches in merging trees (e.g., $A_1 = A_2 = 1$ in network (3-a)) or in the most downstream branches in splitting trees (e.g., $A_2 = A_3 = 1$ in network (3-b)). In **b**, **d**, **f**, the cross-sectional area is the same in the network $A_j = 1$; the flow advection rate is $v_j = 0.0015$ in the most upstream branches in merging trees or in the most downstream branches in splitting trees. Boundary conditions: **a**–**b** (ZF-FF); **c**–**d** (H-H); **e**–**f** (ZF-H)

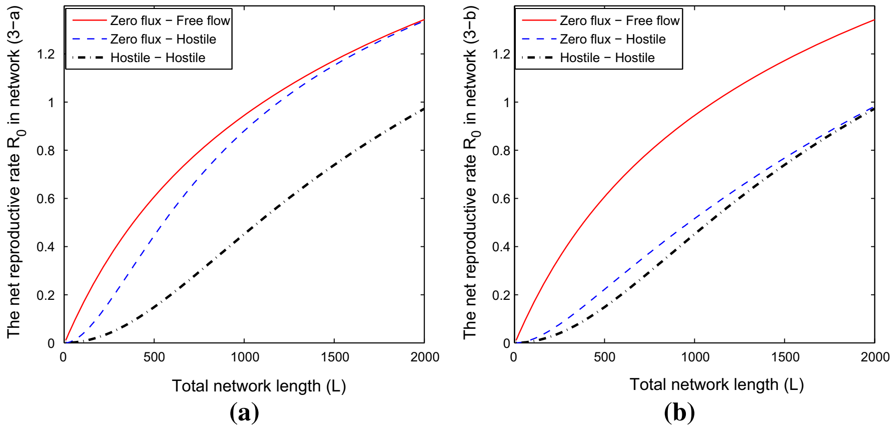



**Fig. 4** The relationship between $\mathcal{R}_0$ and the total length $L$ of the river networks (3-a) and (3-b), from Fig. 3b, d, f

same type of network with the same length, if the total upstream flow discharge is constant, then the network with constant flow velocity yields a larger net reproductive rate than the network with constant cross-sectional areas does (e.g., $R_0$ in network (3-a) is larger in Fig. 3a than in Fig. 3b). This is because there are some channels with high flow velocities in the latter network, which makes the habitat conditions worse for population growth.

### 5.1.2 The Influence of Boundary Conditions on $R_0$

It has been shown that boundary conditions may greatly influence the long-term behavior of a population in river environments, see, e.g., Lam et al. (2016), Sarhad and Anderson (2015). Figure 3a–d shows that when (ZF-FF) or (H-H) boundary conditions are applied, $R_0$ is the same in networks (3-a) and (3-b), in networks (5-a) and (5-b), or in networks (7-a) and (7-b). This seems to indicate that under these boundary conditions, whether the network is a merging tree (e.g., edges join at the downstream end) or a splitting tree (e.g., edges split at the upstream end) does not affect the net reproductive rate, provided that at every junction node only three edges are involved in the merging or splitting phenomenon. Nevertheless, when (ZF-H) boundary conditions are applied, the value of $R_0$ in network (3-a) (or (5-a), (7-a), respectively) is not less than the value of $R_0$ in network (3-b) (or (5-b), (7-b), respectively) (see Fig. 3e–f). This is because when the population is not lost from the upstream and the downstream end is lethal, more branches in the downstream cannot result in better conditions for population persistence. We do not see the exact same phenomenon as above in the networks of 4 branches (networks (4-a,b)). When (ZF-FF) or (H-H) boundary conditions are applied, the 4-branch merging tree (network (4-a)) admits a larger $R_0$ than the 4-branch splitting tree (network (4-b)) does, so having more upstream branches helps population persist if the upstream boundary condition is better for the population than the downstream one (ZF-FF) or if both boundaries are lethal (H-H). Nevertheless, when (ZF-H) boundary conditions are applied, if the total river length is small, then the value of $R_0$ in network (4-a) may be smaller than the one in network (4-b) (see Fig. 3e). Overall, in all these types of river networks with equal branch length, more upstream branches are more beneficial to population persistence or at least do not accelerate population extinction, provided that the upstream ends are not the only boundaries that are subjected to hostile conditions and that the total network length is sufficiently large.

To see the effect of boundary conditions on the net reproductive rate more closely, we focus on the $R_0$ values in networks of 3 branches when the cross-sectional areas are the same throughout the network, and compare the corresponding curves from Fig. 3b, d, f in Fig. 4. It shows that the combination of zero-flux upstream condition and free flow downstream condition yields the largest value of $\mathcal{R}_0$ and that hostile condition at both ends yields the smallest value of $R_0$. When the total length of the network is small, different boundary conditions result in significantly different values of $R_0$. When the total length of the network is large, imposing the hostile condition or the free flow condition at the downstream end does not make much difference to $\mathcal{R}_0$ if more branches are at the upstream (i.e., in network (3-a)) with the same boundary condition, while the upstream conditions do not influence $\mathcal{R}_0$ much if more branches are at the downstream (i.e., in network (3-b)) with the same boundary condition. Therefore, one may need to consider the influence of boundary conditions on the net reproductive rate in a specific river network.

### 5.2 Population Dynamics in Networks Consisting of a Main River and Small Tributaries

A natural river network is composed of a main river and all of its tributaries. In this subsection, we will pay close attention to population dynamics in river networks where one or two tributaries flow into a main river channel, in order to better understand the influence of small tributaries on population persistence or extinction in river networks. In particular, we will consider networks (3-a*) and (4-a*) in Fig. 5. In network (3-a*), a small river channel ($k_2$) flows into the main river channel (consisting of $k_1$ and $k_3$); in network (4-a*), two small river channels ($k_2$ and $k_3$) flow into the main river channel (consisting of $k_1$ and $k_4$).

Hydraulic and physical characteristics in a real river are closely related (see, e.g., Chaudhry 1993; Jin and Lewis 2014). To better explore population dynamics in a

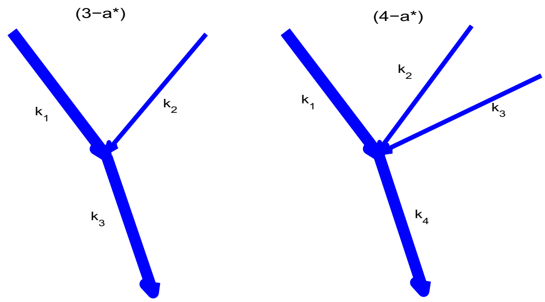



**Fig. 5** River networks where one or two small branches flow into the main river. The arrows represent the direction of the water flow

river network, we incorporate the explicit relation between hydraulic and physical factors into the population model and investigate their effects on the net reproductive rate and the positive steady state (if exists). Assume a constant bottom slope $S_{0j}$, a constant bottom Manning roughness coefficient $n_j$, and a rectangular cross section with constant width $B_j$ in branch $k_j$ of the network. We further assume that the water flow is at the steady state with flow discharge $Q_j$ in $k_j$; hence, there is a uniform flow in $k_j$ Chaudhry (1993). As a result, the water depth $y_j$ in $k_j$ can be approximated by the normal depth defined in (D.2) in "Appendix D":

$$y_j = \left( \frac{Q_j^2 n_j^2}{B_j^2 S_{0j} k^2} \right)^{\frac{3}{10}}, \tag{5.1}$$

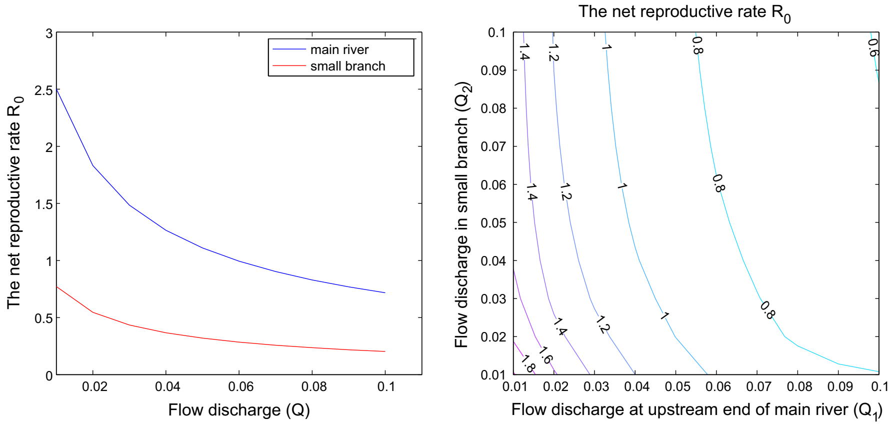
which yields the flow velocity in branch $k_j$ as

$$v_j = \frac{Q_j}{A_j} = \frac{Q_j}{B_j y_j}. \tag{5.2}$$

We then can substitute (5.1) and (5.2) into **(IBVP)** to study how parameters influence population persistence in uniform flows in river networks. The Manning coefficient and the bottom slope are chosen as constants in this subsection: $n_j = 0.2$, $S_{0j} = 0.000001$.

#### 5.2.1 The Influence of the Flow Discharge on $\mathcal{R}_0$

We first consider the influence of the flow discharge on $\mathcal{R}_0$ in network (3-a*). Assume that the length and width of the main river ($k_1$&$k_3$) are $l = l_1 + l_3 = 1600$ and $B_1 = B_3 = 20$, respectively, that the length and width of the small branch ($k_2$) are $l_2 = 800$ and $B_2 = 4$, respectively, and that the bottom slope, the bottom roughness, and biological conditions (diffusion rate, birth and death rates) are the same throughout the network. For simplicity, we assume that the small branch joins the main river at its midpoint. Figure 6a shows how the net reproductive rate $\mathcal{R}_0$ varies with the flow discharge in the main channel and in the small branch if they are not connected. We see that $\mathcal{R}_0$ decreases with the upstream flow discharge, which coincides with previous results of population dynamics in one-dimensional rivers (see, e.g., Jin and Lewis 2014), and that $R_0$ is larger in the main channel than in the small branch. Figure 6b shows the dependence of $\mathcal{R}_0$ on the upstream flow discharge in the main river $Q_1$ and the upstream flow discharge in the small branch $Q_2$. Clearly, $\mathcal{R}_0$ is large when both $Q_1$ and $Q_2$ are small and $\mathcal{R}_0$ is small when both $Q_1$ and $Q_2$ are large. Hence, in a river network, it is still true that low upstream flow discharges help population persist and high upstream flow discharges accelerate population's extinction. Moreover, $R_0$ decreases more rapidly in $Q_1$ than it does in $Q_2$, which implies that, given the same habitat and demography conditions, the upstream flow discharge in the large main river influences global population persistence/extinction more than the upstream flow discharge in the small branch does. Note that in this example the population will be extinct in the small branch if it does not join the main river (see Fig. 6a), but joining the small branch into the main river may help the population persist in the whole network.




**(a)** **(b)**

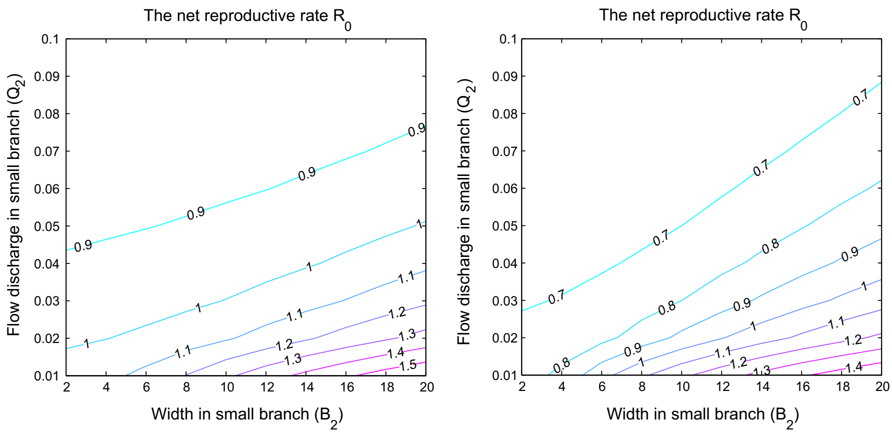
**Fig. 6** The relationship between $\mathcal{R}_0$ and the upstream flow discharges in network (3-a*). Parameters: $D_j = 0.6$, $m_j = 0.0000007$, $r_j = 0.0000093$. **a** $R_0$ in the main river and in the small branch if they are not connected. **b** $R_0$ in network (3-a*); the curves are contour lines for $\mathcal{R}_0$. Boundary conditions: (ZF-FF)

### 5.2.2 The Influence of the Flow Discharge and the Width of the Small Branches on $\mathcal{R}_0$

Next, we assume that the conditions in the main river are constant, but study the influence of the flow discharge ($Q_2$) and the width ($B_2$) of the small branches on population dynamics in the whole network. This can help us know more about what long-term behaviors of a population to expect when one or more small branches are added in or removed from an existing main river. We consider two upstream flow conditions in the main river: (a) $Q_1 = 0.05$, under which the population can persist in the main river ($\mathcal{R}_{0,\text{main}} = 1.109$), and (b) $Q_1 = 0.09$, under which the population will be extinct in the main river ($\mathcal{R}_{0,\text{main}} = 0.768$), if the main river is not connected with a small branch.

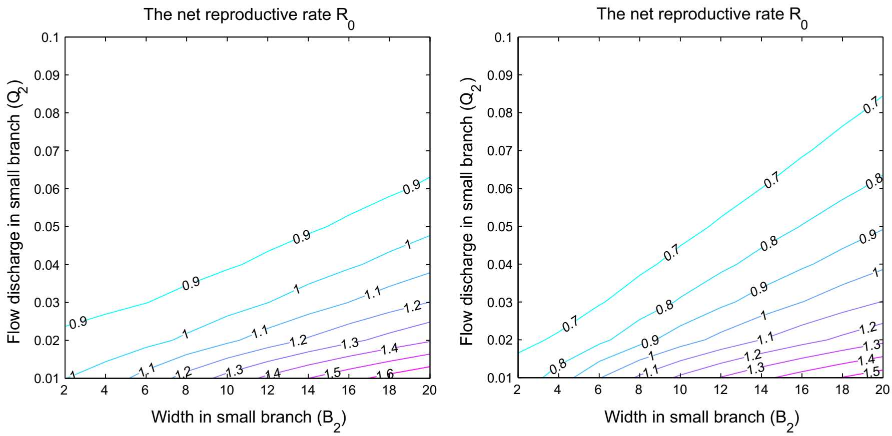
Figure 7 shows the dependence of $\mathcal{R}_0$ on $Q_2$ and $B_2$ in network (3-a*). Both figures show the same phenomenon: A population may grow better or worse if a new small branch joins the main river; in order to increase $\mathcal{R}_0$ or help the population persist in the whole network, low upstream flow discharge and large width, or equivalently, low flow discharge per unit width $Q_2/B_2$, in the small branch, should be imposed. If the conditions in the main river (for population growth) become worse (e.g., from Fig. 7a to b), then lower $Q_2/B_2$ in the small branch is required in order for the population to persist (or $\mathcal{R}_0 > 1$) in the whole network.

We then consider network (4-a*), where two small branches ($k_2$ and $k_3$) join the main river ($k_1$&$k_4$) at its midpoint. For simplicity, we assume that all the conditions in the main river and in the small branches are the same as those in the above network (3-a*). The dependence of $\mathcal{R}_0$ on the flow discharge $Q_2(= Q_3)$ and the width $B_2(= B_3)$ in the small branches is shown in Fig. 8, which again indicates that low upstream discharge and large width in the small branches help the population persist in the whole network. Comparing Figs. 7 and 8, we see that lower flow discharge per unit




**(a)** **(b)**

**Fig. 7** The dependence of $\mathcal{R}_0$ on the flow discharge $Q_2$ and the width $B_2$ in the small branch ($k_2$) in network (3-a*). The curves are contour lines for $\mathcal{R}_0$. Parameters: $D_j = 0.6$, $m_j = 0.0000007$, $r_j = 0.0000093$, $B_1 = B_3 = 20$. **a** $Q_1 = 0.05$; **b** $Q_1 = 0.09$. Boundary conditions: (ZF-FF)




**(a)** **(b)**

**Fig. 8** The dependence of $\mathcal{R}_0$ on the flow discharge and the width in the small branches ($k_2$ and $k_3$) in network (4-a*). Parameters: $D_j = 0.6$, $m_j = 0.0000007$, $r_j = 0.0000093$, $B_1 = B_4 = 20$, $B_2 = B_3$, $Q_2 = Q_3$. **a** $Q_1 = 0.05$; **b** $Q_1 = 0.09$. Boundary conditions: (ZF-FF)

width $Q_2/B_2$ in small branches is needed for $\mathcal{R}_0$ to go beyond 1 in network (4-a*) than in network (3-a*), but when $Q_2/B_2$ is sufficiently small, $\mathcal{R}_0$ can be larger in network (4-a*) than in network (3-a*). This implies that the threshold conditions for population persistence in a large network may be stronger than those in a small network, but the population may grow better in the large network once it persists.

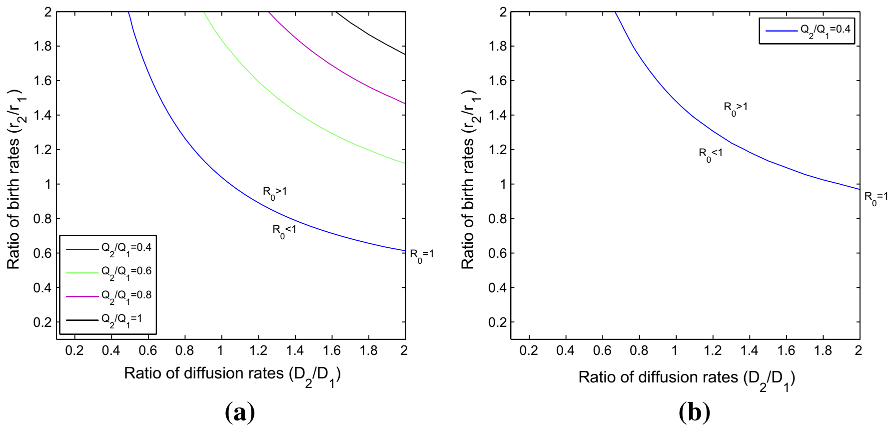


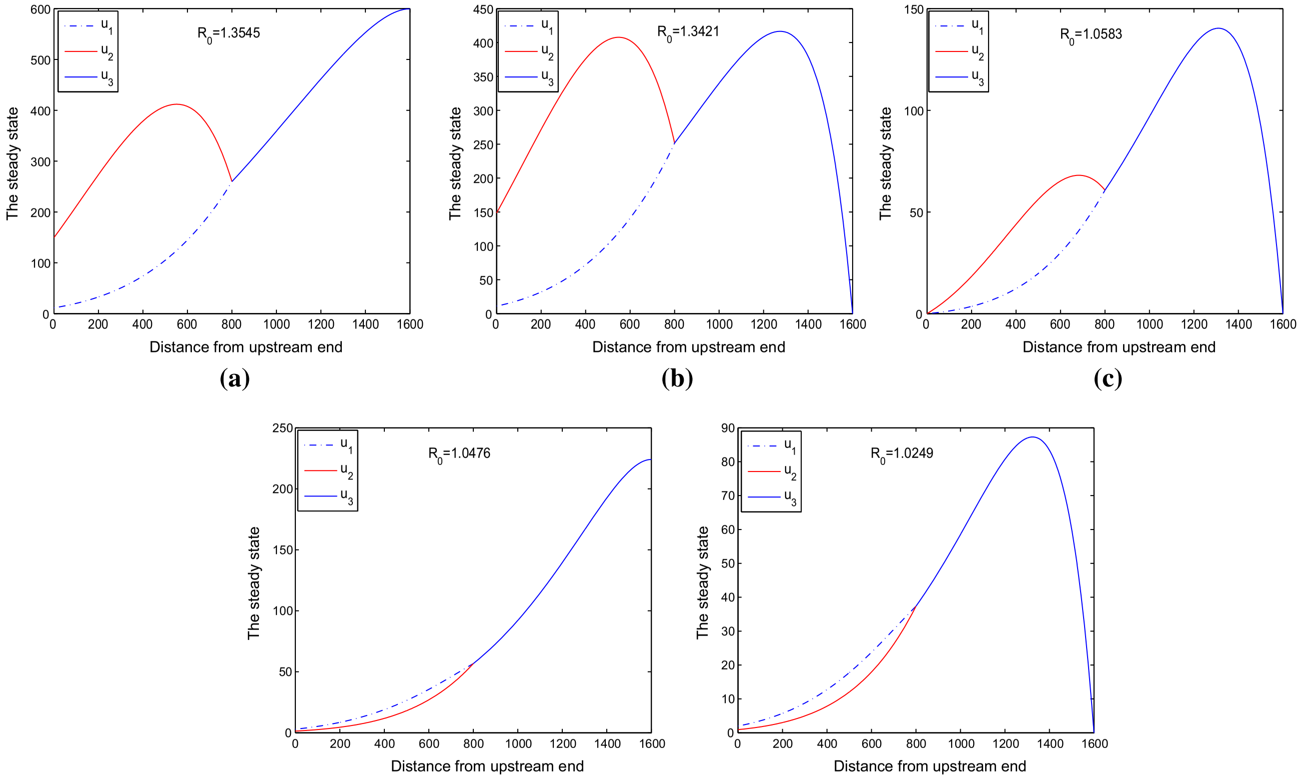

**Fig. 9** The regions for persistence ($\mathcal{R}_0 > 1$) and extinction ($\mathcal{R}_0 < 1$) in parameter space in networks (3-a*) and (4-a*). Parameters: $m_j = 0.0000007$, $Q_1 = 0.05$. **a** In network (3-a*), $D_1 = D_3 = 0.6$, $r_1 = r_3 = 0.0000093$, $B_1 = B_3 = 20$, $B_2 = 4$; **b** In network (4-a*), $D_1 = D_4 = 0.6$, $r_1 = r_4 = 0.0000093$, $B_1 = B_4 = 20$, $B_2 = B_3 = 4$, $D_2 = D_3$, $r_2 = r_3$, $Q_2 = Q_3$. Boundary conditions: (ZF-FF). The curves correspond to $\mathcal{R}_0 = 1$ under corresponding parameter conditions

### 5.2.3 The Influence of the Flow Discharge and Biological Conditions on $\mathcal{R}_0$

Not only the physical and hydraulic features but also biological characteristics in the tributaries may be different from those in the main river. We further consider the co-influence of the flow discharge and biotic factors on population dynamics in networks (3-a*) and (4-a*). We assume constant flow discharge, diffusion rate, and birth rate in the main river, but allow for variations of these parameters in the small branches, in order to be applicable for different types of tributaries in river networks. Figure 9 shows the regions for population persistence ($\mathcal{R}_0 > 1$) or extinction ($\mathcal{R}_0 < 1$) in the $D_2/D_1$-$r_2/r_1$ plane under different flow conditions. It turns out that given constant conditions in the main river, the larger the diffusion rate $D_2$ or the birth rate $r_2$ is, or the smaller the flow discharge $Q_2$ is in the small river branches, the easier it is for the population to persist ($\mathcal{R}_0 > 1$) in the whole network of (3-a*) or (4-a*). Comparing the two figures in Fig. 9, we see that the parameter region for $\mathcal{R}_0 > 1$ in network (4-a*) is smaller than that in network (3-a*) under the same flow conditions. This confirms our previous observation that if more small rivers flow into the main river, then better conditions in the small branches may be needed to ensure population persistence in the whole river network.

### 5.2.4 The Globally Attractive Positive Steady State of (IBVP) in Network (3-a*)

We have proved in Theorem 3.3 (or Corollary 4.2) that if the population persists, then it will eventually be stabilized at a positive steady state. We plot the spatial profile of the globally attractive positive steady state (when $\mathcal{R}_0 > 1$) of **(IBVP)** in network (3-a*), under different flow and boundary conditions, see Fig. 10. In simulations, we assume that the birth rate and the diffusion rate are higher in the small branch than




(a) (b) (c) (d) (e)

**Fig. 10** The positive steady state of **(IBVP)** in network (3-a*). Parameters: $m_j = 0.0000007$, $Q_1 = 0.05$, $D_1 = D_3 = 0.6$, $r_1 = r_3 = 0.0000093$, $l_j = 800$, $B_1 = B_3 = 20$, $B_2 = 4$; $D_2 = 1.2D_1$, $r_2 = 1.2r_1$; **a–c** $Q_2 = 0.1Q_1$; **d–e** $Q_2 = 0.4Q_1$. Boundary conditions: **a**, **d** (ZF-FF); **b**, **e** (ZF-H); **c** (H-H). Note that when $Q_2 = 0.4Q_1$ and (H-H) boundary conditions are applied, $\mathcal{R}_0 = 0.9301$ and no positive steady state exists those in the main river. Results show that when $\mathcal{R}_0$ is very large, the population density is high in the small branch (in the upstream) and in the downstream main river, but the population is mainly distributed in the downstream main river when $\mathcal{R}_0$ is only slightly larger than 1. We also calculated the next-generation distribution (i.e., the eigenfunction of the next-generation operator corresponding to $R_0$) in these cases and obtained similar profiles as those of the steady states in Fig. 10. Thus, we may say that if a population can persist in such a river network, then one should always be able to find a high population density in the downstream main river and that if the population persists very well then high population density could also be found in the upstream branch where the growth conditions are the best.

## 6 Discussion

Rivers connect to each other to form networks in the natural world. The geometric structure in river networks varies from network to network; the physical and hydraulic features in a river network vary from branch to branch. As a result, these characteristics highly influence the flow profile in a river network and hence the dynamics of the ecosystem in the network. In river population models, the rivers are often treated as one-dimensional intervals (see, e.g., Speirs and Gurney 2001; Mckenzie et al. 2012; Jin and Lewis 2011; Lam et al. 2016; Lutscher et al. 2005), or as discrete patches for different branches in a network (see, e.g., Fagan 2002; Grant et al. 2010; Goldberg et al. 2010; Mari et al. 2014). Only in a few recent works, the geometric structure of continuous river networks has been incorporated into river population models: Integro-differential equations Ramirez (2012) and reaction–diffusion–advection (RDA) equations (Sarhad and Anderson 2015; Sarhad et al. 2014; Vasilyeva 2019) were used to describe population dynamics in river networks. The conditions for population persistence were established for linear (or the linearized) systems in these works, and the existence and uniqueness of a positive steady state were also established in the most recent work Vasilyeva (2019) for an RDA model with a logistic growth rate.

In this work, we considered an RDA model for populations living in river networks with general tree structures. We allowed for variations of physical, hydraulic, and demographic conditions in the edges of the network and assumed different diffusion rates, advection rates, and growth functions in different edges. In previous works Sarhad and Anderson (2015), Sarhad et al. (2014), Vasilyeva (2019), these parameters were assumed to be constants throughout the network and their methods highly depended on this simplification as it allowed them to reduce the RDA model into a diffusion model, and hence applying their methods to our model should not be trivial if not impossible. We considered general boundary conditions ((2.5) and (2.7)) in **(IBVP)**, which not only include any combination of zero-flux, free flow, or hostile conditions as considered in Ramirez (2012), Sarhad and Anderson (2015), Sarhad et al. (2014), Vasilyeva (2019), but also allow for more general possibilities as those in Lam et al. (2016), where the population flux at the upstream or downstream boundary may be proportional to the population density there. The growth functions in our model were assumed to be the general type of monostable functions that have often been used in one-dimensional river population models. The logistic function used in

Vasilyeva (2019) can be considered as an example. Most of the results in Sarhad et al. (2014) and the results in Sarhad and Anderson (2015) were established in radially symmetric trees, in which all tree features, including edge lengths, sectional areas, junction conditions, and boundary conditions, depend only on the distance to the root. The network considered in Vasilyeva (2019) is not a radial tree, but it is a simple Y-shaped tree with 3 edges in total. In our model, the network was assumed to have the general tree structure, which is not restricted to be radially symmetric or binary.

Fundamental analysis for parabolic and elliptic equations on networks has not been new, see, e.g., the series of works by J. von Below. As there have been only few studies on population dynamics in river networks, it has not been made clear what existing theories are available for RDA models in river networks and/or what new theories need to be generated. By adapting theories for parabolic and elliptic equations on intervals and/or networks (Mugnolo 2012; Arendt et al. 2014; Fijavž et al. 2007; Protter and Weinberger 1967; von Below 1988a, 1991, 1994; Ladyzenskaja et al. 1968; Solonnikov 1965; Pao 1992; Ye et al. 2011), we developed the fundamental theories for the parabolic and elliptic problems on river networks corresponding to **(IBVP)**, such as the strong maximum principle, Hopf boundary lemma, comparison principle, the existence, uniqueness, and $L^p$ and Schauder estimates of solutions, as well as the theory of the existence, uniqueness, and positivity of solutions for the nonlinear problem **(IBVP)**. We expect that the theories in "Appendix A" will serve as a theoretical basis for future studies on RDA models for populations living in river networks. In fact, our theories have already been applied in two recent works (Du et al. 2019, 2018).

We established the existence of the principal eigenvalue $\lambda^*$ of the corresponding eigenvalue problem (3.5). By using the comparison principle, we proved that an RDA model (with monostable-type growth functions) in metric trees has the same long-term behaviors as in a one-dimensional river (see, e.g., Mckenzie et al. 2012): The population density converges to 0 if $\lambda^* \leq 0$ and there exists a unique positive steady state that is globally attractive if $\lambda^* > 0$. While the existence and uniqueness of the positive steady state were proved in a simpler network in Vasilyeva (2019), we have obtained its global attractivity in general trees. In fact, "population persistence" in this work represents the situation where the population asymptotically approaches the unique positive steady state, while it represents instability of the trivial solution in previous works on river networks (Ramirez 2012; Sarhad and Anderson 2015; Sarhad et al. 2014; Vasilyeva 2019).

Although the principal eigenvalue of the eigenvalue problem can be used to mathematically define population persistence or extinction, the net reproductive rate is a biologically more significant quantity that is often used to determine population dynamics, as it represents the average number of offsprings that a single individual produces during its lifetime. The net reproductive rate has not been established in previous studies in population models on river networks. We extended the definition of the next-generation operator for one-dimensional river models (see Mckenzie et al. 2012) to our RDA model in river networks and used it to define the net reproductive rate $R_0$. We were also able to prove that $R_0$ can be equivalently used to determine population persistence ($\mathcal{R}_0 > 1$) and extinction ($\mathcal{R}_0 \leq 1$) in river networks. It is difficult to calculate $R_0$ based on its original definition as the spectral radius of the next-generation operator. The method used in Mckenzie et al. (2012) to calculate $R_0$ for a one-dimensional river model cannot be applied to our model. We then converted the calculation of $\mathcal{R}_0$ to calculation of the principal eigenvalue of a new generalized eigenvalue problem by using the theory in Wang and Zhao (2012), and we also provided a method to approximate the eigenfunction of the next-generation operator corresponding to $R_0$, which we call the next-generation distribution. Due to the generality of our model, it is impossible to obtain an explicit formula or an approximation of $\lambda^*$ or $R_0$ in terms of the model parameters. However, we can discretize the eigenvalue problems to numerically calculate them. Noting the biological meaning of $R_0$, by studying the dependence of $R_0$ on specific parameters, we can better understand the influence of habitat and demography factors on population persistence or extinction. The next-generation distribution can also help us determine the good or bad regions in a river network.

The results in our numerical simulations coincide with existing findings in one-dimensional rivers or in radial trees: In a given type of river network, it is easier for the population to persist if the total river length is larger, the flow discharge/advection is lower, or the diffusion rate or the growth rate is higher, see also, e.g., Sarhad et al. (2014), Lutscher et al. (2005), Jin and Lewis (2014). We also found that in radial trees with the same total length, the net reproductive rate is higher in the tree with lower order (i.e., less branches), provided that all the biotic and physical conditions are the same. This implies that a population can grow better in a radial river with simpler structure if the river length is given. However, if the river networks do not admit the radial symmetry, then this rule is no longer true and the persistence situation of the population highly depends on the structures of the networks in concern. This verifies the different influences of the geometric structures of radial and non-radial trees on population dynamics and the necessity to study population models in general trees.

In our simulations, we particularly compared population dynamics in the situations where one or two small branches flow into a main river. This special scenario can be considered as a simplification of the real problem of adding or removing one branch to or from a network, which may occur when one upstream branch in the dessert disappears because of drought or when human beings artificially attach a new upstream or downstream branch to a network for some economic, ecological, or other reasons. In such scenarios, one may naturally ask questions, such as how will such a phenomenon or activity influence the long-term behaviors of a population in the network, will the loss of a branch in the dessert cause the extinction of a species, will a new branch attached to the network be beneficial to persistence of a species. Our results show that stronger (or better) conditions in the small branch(es) are required for a population to persist in the network where two small branches flow into the main river than in the network where only one small branch is connected to the main river. However, if the population can persist in both networks, then it persists better in the larger network (i.e., $R_0$ is larger in the larger network than in the smaller one). This phenomenon, to some extent, confirms our intuitive understanding that if the lost branch in the desert does not have suitable conditions for population growth, then it is not necessary to worry that losing it will cause the population to be extinct faster, and that if the new attached channel is endowed with favorable conditions, then the population can grow better than before.

The theoretical results derived in this work (in Sects. 2–4 and "Appendix A") hold for any general finite trees. The simulations in this work are all for small networks (of no more than 7 branches) for calculation simplicity. We note that the phenomena observed in the radial trees should be generally true for radial trees of larger order. However, due to the complexity of non-radial trees, we would expect that the phenomena observed in non-radial trees only apply in larger trees with the same or similar structures as those in our examples. The influence of specific hydraulic, physical, and biological factors on population dynamics in non-radial trees highly depends on the geometric structure of the network.

Our theory for the principal eigenvalue and associated eigenfunction depends on the tree structure of the network, which allows for the possibility of writing the differential operator in (2.3) into a self-adjoint operator. If the network is not a tree, then we cannot establish the principal eigenvalue by this method and the persistence theory still remains open. As in Vasilyeva (2019), we assumed that the whole wetted cross-sectional area is habitable. When the habitable areas are smaller than the wetted cross-sectional areas Sarhad et al. (2014), it would also be interesting to understand population dynamics in general networks with heterogeneity. Another potential future work could be better estimation of the principal eigenvalue $\lambda^*$ of the eigenvalue problem on networks. The dynamics of interacting species in river networks could also be an interesting future problem (see, e.g., Cuddington and Yodzis 2002).

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## Appendix A Theory of Parabolic and Elliptic Equations on Networks

### A.1 The Strong Maximum Principle and Comparison Principle

In this subsection, we establish the strong maximum principle and comparison principle for parabolic equations on metric graphs, which are fundamental in the investigation of existence, uniqueness, and positivity of solutions to the nonlinear problem **(IBVP)**.

The following strong maximum principle is an analogue of the classical one for equations on open subsets in Euclidian spaces.

**Lemma A.1** *Assume that $c(x,t) \geq 0$ and is bounded from above on $\Omega$. Let $u \in C(\Omega) \cap C^{2,1}(\Omega_p)$ satisfy*

$$\frac{\partial u_j}{\partial t} - D_j \frac{\partial^2 u_j}{\partial x_j^2} + v_j \frac{\partial u_j}{\partial x_j} + c_j(x_j,t)u_j \leq 0 \ (\geq 0),\ \ x_j \in (0,l_j),\ \ j \in I_{N-1},\ \ t \in (0,T],$$

*and*

$$u_{i_1}(e_i,t)=\cdots=u_{i_m}(e_i,t),$$
$$\sum_{j=i_1}^{i_m} d_{ij}A_jD_j\frac{\partial u_j}{\partial x_j}(e_i,t)\le 0\ (\ge 0),\quad \forall e_i\in E_{\mathrm{r}},\ t\in(0,T].$$

*Suppose that* $u\le M$ $(u\ge m)$ *on* $\Omega$ *and* $u(x_0,t_0)=M$ $(u(x_0,t_0)=m)$ *at some point* $(x_0,t_0)\in\Omega_p$. *If* $c(x,t)\not\equiv 0$, *suppose that* $M\ge 0$ $(m\le 0)$. *Then*

$$u=M\ (u=m)\ \text{ on } G\times[0,t_0].$$

***Proof*** Suppose that $u(x_0,t_0)=M$ at some point $(x_0,t_0)\in\Omega_p$. We distinguish two cases: (i) $x_0\notin E_{\mathrm{r}}$; (ii) $x_0\in E_{\mathrm{r}}$.

In Case (i), clearly $x_0$ is an interior point of some edge $k_j$. The direct application of the strong maximum principle for Euclidean domains (see, for example, Protter and Weinberger (1967), Theorem 4, Chapter 3) gives

$$u_j(x_j,t)=M,\quad \forall(x_j,t)\in[0,l_j]\times[0,t_0].$$

Let $k_h$ be an arbitrary edge such that $k_h\cap k_j=\{e_i\}$, where $e_i$ is an end point of $k_j$. If there exists an interior point $y_0$ of $k_h$ such that $u_h(y_0,t_0)=M$, then

$$u_h(x_h,t)=M,\quad \forall(x_h,t)\in[0,l_h]\times[0,t_0], \tag{A.1}$$

due to the strong maximum principle for domains. If such interior maximum point does not exist, then it is necessary that

$$u_h(x_h,t_0)<M,\quad \forall x_h\in(0,l_h). \tag{A.2}$$

Thus, we can claim that for some $0<\hat{t}<t_0$, there holds

$$u_h(x_h,t)<M,\quad \forall(x_h,t)\in(0,l_h)\times(\hat{t},t_0). \tag{A.3}$$

Suppose that such a claim is false. Then we can find a sequence $\{(\hat{x}_n,\hat{t}_n)\}_{n=1}^{\infty}$ with $\hat{x}_n\in(0,l_h)$, $\hat{t}_n<\hat{t}_{n+1}$ for all $n\ge 1$ and $\hat{t}_n\to t_0$ as $n\to\infty$ such that $u_h(\hat{x}_n,\hat{t}_n)=M$ for all $n\ge 1$. By the strong maximum principle for domains again, one has $u_h(x_h,\hat{t}_n)=M$ for all $x_h\in[0,l_h]$. Since $\hat{t}_n\to t_0$ as $n\to\infty$ and $u_h$ is continuous on $[0,l_h]\times[0,t_0]$, it easily follows that (A.1) holds, which contradicts (A.2). Hence, claim (A.3) is proved. In view of (A.3) and the fact that $u_h(x_h,t)$ attains its maximum $M$ at the boundary point $(e_i,t_0)$ of the region $[0,l_h]\times(\hat{t},t_0)$, one then applies the classical Hopf boundary lemma for Euclidean domains (see (Protter and Weinberger 1967, Theorem 3, Chapter 3)) to conclude that $d_{hi}\frac{\partial u_h}{\partial x_h}(e_i,t_0)>0$. Recall that $M$ is the maximum value of $u$ on $\Omega$. So for any $j=i_1,\ldots,i_m$ with $j\ne h$ such that $k_j\cap k_h\ne\varnothing$, we have $d_{ij}\frac{\partial u_j}{\partial x_j}(e_i,t_0)\ge 0$. Therefore, it holds

$$\sum_{j=i_1}^{i_m} d_{ij} A_j D_j \frac{\partial u_j}{\partial x_j}(e_i, t_0) > 0,$$

which is impossible due to our assumption. This contradiction shows that (A.1) must hold. As $G$ is connected, we can assert that $u = M$ in $G \times [0, t_0]$.

We now consider Case (ii). Take $k_j$ to be an arbitrary edge such that $x_0$ is its endpoint and $x_0 \in E_\mathrm{r}$. By what was proved in Case (i), we can suppose that $u_j(x_j, t_0) < M$, $\forall x_j \in (0, l_j)$. However, the same arguments as in Case (i) lead to a contradiction. Thus, $u_j(x_j, t) = M$ for all $(x_j, t) \in [0, l_j] \times [0, t_0]$ and in turn $u = M$ in $G \times [0, t_0]$ by the arbitrariness of $k_j$. □

We remark that von Below (1991), Theorem 1 covers the special case of Lemma A.1, where $c(x, t) \equiv 0$ and

$$\sum_{j=i_1}^{i_m} d_{ij} A_j D_j \frac{\partial u_j}{\partial x_j}(e_i, t) = 0, \ \forall e_i \in E_\mathrm{r}, \ t \in (0, T].$$

Hence, our result is more general and it is useful when dealing with upper and/or lower solutions. As a direct application of Lemma A.1 as the classical Hopf lemma for Euclidean domains (see, for example, Protter and Weinberger 1967, Theorem 3, Chapter 3), we have the following Hopf boundary lemma for networks.

**Lemma A.2** *Assume that $c(x, t) \geq 0$ and is bounded from above on $\Omega$. Let $u \in C(\Omega) \cap C^{2,1}(\Omega_p)$ satisfy*

$$\frac{\partial u_j}{\partial t} - D_j \frac{\partial^2 u_j}{\partial x_j^2} + v_j \frac{\partial u_j}{\partial x_j} + c(x_j, t) u_j \leq 0 \ (\geq 0), \quad x_j \in (0, l_j), \ j \in I_{N-1}, \ t > 0.$$

*Suppose that $u$ is continuously differentiable at some point $(e_i, t_0) \in E_\mathrm{b} \times (0, T]$, $u(e_i, t_0) = M$ ($u(e_i, t_0) = m$), $u(x, t) < M$ ($> m$) for all $(x, t) \in \Omega_p$, and $e_i$ is a vertex on $k_j$. If $c \not\equiv 0$, assume that $M \geq 0$ ($m \leq 0$). Then $d_{ij} u_{x_j}(e_i, t_0) > 0$ ($< 0$).*

As a corollary of Lemmas A.1 and A.2, we immediately obtain the following comparison principle.

**Lemma A.3** *Assume that $c(x,t)$ is bounded on $\Omega$. Let $u \in C(\Omega) \cap C^{2,1}(\Omega_p)$ satisfy*

$$\begin{cases} \dfrac{\partial u_j}{\partial t} - D_j \dfrac{\partial^2 u_j}{\partial x_j^2} + v_j \dfrac{\partial u_j}{\partial x_j} + c_j(x_j,t)u_j \geq 0, & x_j \in (0,l_j),\ j \in I_{N-1},\ t \in (0,T), \\ \alpha_{j,1} u_j(e_i,t) - \beta_{j,1} \dfrac{\partial u_j}{\partial x_j}(e_i,t) \geq 0, & \forall e_i \in E_{\mathrm{u}},\ t \in (0,T), \\ \alpha_{j,2} u_j(e_i,t) + \beta_{j,2} \dfrac{\partial u_j}{\partial x_j}(e_i,t) \geq 0, & \forall e_i \in E_{\mathrm{d}},\ t \in (0,T), \\ u_{i_1}(e_i,t) = \cdots = u_{i_m}(e_i,t), & \forall e_i \in E_{\mathrm{r}},\ t \in (0,T), \\ \displaystyle\sum_{j=i_1}^{i_m} d_{ij} A_j D_j \dfrac{\partial u_j}{\partial x_j}(e_i,t) \geq 0, & \forall e_i \in E_{\mathrm{r}},\ t \in (0,T), \\ u_j(x_j,0) \geq 0, & x_j \in (0,l_j),\quad j \in I_{N-1}, \end{cases} \tag{A.4}$$

*and assume that $\frac{\partial u_j}{\partial x_j}(e_i,t)$ exists for $t \in (0,T]$ and $e_i \in E_{\mathrm{b}}$ if $\beta_{j,s} \neq 0$ for some $j \in I_{N-1}$, $s \in \{1,2\}$. Then $u(x,t) \geq 0$ for all $(x,t) \in \Omega$. If $u(x,0) \not\equiv 0$, then $u(x,t) > 0$ for all $(x,t) \in G \backslash E_0 \times (0,T]$.*

***Proof*** Denote $v(x,t) = e^{-\ell t} u(x,t)$, and take the constant $\ell > 0$ to be large so that $\ell + c > 0$ on $\Omega$. Elementary computation gives $v \in C(\Omega) \cap C^{2,1}(\Omega_p)$ satisfying

$$\begin{cases} \dfrac{\partial v_j}{\partial t} - D_j \dfrac{\partial^2 v_j}{\partial x_j^2} + v_j \dfrac{\partial v_j}{\partial x_j} + [c_j(x_j,t) + \ell] v_j \geq 0, & x_j \in (0,l_j),\ j \in I_{N-1},\ t \in (0,T), \\ \alpha_{j,1} v_j(e_i,t) - \beta_{j,1} \dfrac{\partial v_j}{\partial x_j}(e_i,t) \geq 0, & \forall e_i \in E_{\mathrm{u}},\ t \in (0,T), \\ \alpha_{j,2} v_j(e_i,t) + \beta_{j,2} \dfrac{\partial v_j}{\partial x_j}(e_i,t) \geq 0, & \forall e_i \in E_{\mathrm{d}},\ t \in (0,T), \\ v_{i_1}(e_i,t) = \cdots = v_{i_m}(e_i,t), & \forall e_i \in E_{\mathrm{r}},\ t \in (0,T), \\ \displaystyle\sum_{j=i_1}^{i_m} d_{ij} A_j D_j \dfrac{\partial v_j}{\partial x_j}(e_i,t) \geq 0, & \forall e_i \in E_{\mathrm{r}},\ t \in (0,T), \\ v_j(x_j,0) \geq 0, & x_j \in (0,l_j),\quad j \in I_{N-1}. \end{cases} \tag{A.5}$$

It follows from Lemmas A.1 and A.2 that $\min\limits_{\Omega} v(x,t) = m \geq 0$, which implies $u(x,t) \geq 0$ on $\Omega$. When $u(x,0) \not\equiv 0$ (equivalently, $v(x,0) \not\equiv 0$), suppose that $u_j(x_*,t_*) = 0$ for some $(x_*,t_*) \in \Omega_p$. Then $v_j(x_*,t_*) = 0 = \min_\Omega v(x,t)$, which implies $v \equiv 0$ on $\Omega$ by Lemma A.1, a contradiction. Thus, $u(x,t) > 0$ for all $(x,t) \in \Omega_p$. Additionally, Lemma A.2 implies that $u(x,t) > 0$ for all $(x,t) \in E_{\mathrm{b}} \backslash E_0 \times (0,T]$. □

We remark that von Below (1994), Theorem 1 states another type of comparison principle for parabolic problems on graphs.

### A.2 Linear Parabolic Problem

In this subsection, we aim to establish the existence, uniqueness, and $L^p$ and Schauder estimates of solutions to the following linear parabolic problem:

$$\begin{aligned}\frac{\partial u_j}{\partial t} &= D_j \frac{\partial^2 u_j}{\partial x_j^2} - v_j \frac{\partial u_j}{\partial x_j} + c_j(x_j, t)u_j \\ &\quad + g_j(x_j, t), \ \ x_j \in (0, l_j), \ \ j \in I_{N-1}, \ \ t \in (0, T),\end{aligned} \tag{A.6}$$

associated with the initial condition, boundary and interior connection conditions:

$$(2.4), \ (2.5), \ (2.7), \ \text{ and } (2.10), \tag{A.7}$$

where $T > 0$ is a fixed number.

We would like to mention that when the initial condition $u^0$ is smooth and satisfies compatibility conditions, von Below (1988a) already studied the solvability of (A.6)–(A.7). Here we want to discuss the same issue for the initial data $u^0 \in L^p(G)$ $(p > 1)$ by appealing to the semigroup theory used in Mugnolo (2012), Arendt et al. (2014), Fijavž et al. (2007). To this end we need to make a transformation so that problems (A.6)–(A.7) can be written in the form that the framework of Mugnolo (2012) can apply.

Let

$$p_j(x_j) = \eta_j e^{-\frac{v_j}{D_j}x_j}, \qquad \zeta_j(x_j) = \frac{p_j(x_j)}{D_j}, \tag{A.8}$$

where $\eta_j$ is a constant to be determined on edge $k_j$. Then (A.6) can be written as

$$\frac{\partial u_j}{\partial t} = \mathcal{A}_j u_j + c_j(x_j, t)u_j + g_j(x_j, t), \ \ x_j \in (0, l_j), \ \ j \in I_{N-1}, \ \ t \in (0, T), \tag{A.9}$$

where

$$\mathcal{A}_j = \frac{1}{\zeta_j(x_j)} \frac{\partial}{\partial x_j}\left[p_j(x_j)\frac{\partial}{\partial x_j}\right]. \tag{A.10}$$

Choose one upstream vertex, and reorder the vertices and edges such that the chosen vertex is $e_1$, the edge connecting to $e_1$ is $k_1$, and the other endpoint $e_2$ of $k_1$ connects to edges $k_2$, $k_3$, …, and $k_m$. Then at $e_2$, interface condition (2.10b) becomes $\sum_{j=1}^m d_{2j} A_j D_j \frac{\partial u_j}{\partial x_j}(e_2) = 0$. Define $\eta_1 = 1$ on the edge $k_1$. Choose suitable $\eta_2$, …, $\eta_m$ such that

$$A_1 D_1 : A_2 D_2 : \cdots : A_m D_m = p_1(e_2) : p_2(e_2) : \cdots : p_m(e_2),$$

where $p_j(e_2) = p_j(0)$ or $= p_j(l_j)$ depending on whether $e_2$ is the starting point or ending point of $k_j$. Then the interface condition at $e_2$ is equivalent to $\sum_{j=1}^m d_{2j} p_j(e_2) \frac{\partial u_j}{\partial x_j}(e_2) = 0$. Since $G$ is a tree, we can similarly choose the values for other $\eta_j$'s and rewrite interface condition (2.10b) at all interior vertices as

$$\sum_{j=i_1}^{i_m} d_{ij} p_j(e_i) \frac{\partial u_j}{\partial x_j}(e_i) = 0. \tag{A.11}$$

Introduce the inner product for functions $\psi,\ \phi \in L^2(G)$ as

$$\langle \psi, \phi \rangle = \sum_{j=1}^{N-1} \int_0^{l_j} \zeta_j(x_j) \psi_j \phi_j \mathrm{d}x_j. \tag{A.12}$$

Then the differential operator $\mathcal{A}$ with the domain given as in Mugnolo (2012), Lemma 4.11 is self-adjoint with respect to $\langle \cdot, \cdot \rangle$, and similar analysis as in Mugnolo (2012) shows that $\mathcal{A}$ generates a compact, contractive, and positive strongly continuous semigroup.

Denote

$$g(x,t) = g_j(x_j, t), \quad x_j \in (0, l_j),\ \ j \in I_{N-1},\ \ t \in (0, T).$$

We now state the following solvability result, and $L^p$ and Schauder estimates for problems (A.6)–(A.7).

**Theorem A.4** *Assume that $c \in L^\infty(\Omega)$, $g \in L^p(\Omega)$ for fixed $p > 1$. Then the initial boundary value problems (A.6)–(A.7) are well-posed on $L^p(G)$, i.e., for any initial data $u^0 \in L^p(G)$, (A.6)–(A.7) admit a unique strong solution $u \in W_p^{2,1}(\Omega)$ (for all $t > 0$) that continuously depends on the initial data. Moreover, the following estimates hold.*

(i) *If $u^0 \in W_p^2(G)$, then the unique solution $u$ satisfies*

$$\|u\|_{W_p^{2,1}(\Omega)} \le C(\|g\|_{L^p(\Omega)} + \|u^0\|_{W_p^2(G)})$$

*for some constant $C > 0$ independent of $u,\ u^0,\ g$.*

(ii) *If $c \in C^{\alpha,\alpha/2}(\Omega)$, $g \in C^\alpha(\Omega)$, $u^0 \in C^{2+\alpha}(G)$ for some $\alpha \in (0,1)$ and $u^0$ satisfies (A.7) at $E_\mathrm{b} \times \{0\}$ and (2.10b) at $E_\mathrm{r} \times \{0\}$, and $[D_j \frac{\partial^2 u_j^0}{\partial x_j^2} - v_j \frac{\partial u_j^0}{\partial x_j} + c_j(\cdot,0)u_j^0 + g_j(\cdot,0)](e_i) = [D_h \frac{\partial^2 u_h^0}{\partial x_h^2} - v_h \frac{\partial u_h^0}{\partial x_h} + c_j(\cdot,0)u_h^0 + g_h(\cdot,0)](e_i)$ when $k_j \cap k_h = \{e_i\}$, then the unique solution $u \in C^{2+\alpha,1+\frac{\alpha}{2}}(\Omega)$ and satisfies*

$$\|u\|_{C^{2+\alpha,1+\frac{\alpha}{2}}(\Omega)} \le C(\|g\|_{C^\alpha(\Omega)} + \|u^0\|_{C^{2+\alpha}(G)})$$

*for some constant $C > 0$ independent of $u,\ u^0,\ g$.*

***Proof*** Note that (A.6) with interface condition (2.10b) can be written as (A.9) with condition (A.11), and the differential operator $\mathcal{A}$ is self-adjoint and generates a compact, contractive, and positive strongly continuous semigroup. Thus, by adjusting the scalar product to (A.12) and defining corresponding functions and operators based on the boundary conditions in (A.7), the analysis in Mugnolo (2012) (see also Arendt et al. 2014; Fijavž et al. 2007) can be borrowed to show that problems (A.6)–(A.7) with the initial data $u^0 \in L^p(G)$ have a unique classical solution for $t > 0$ that continuously depends on the initial data.

The Schauder estimates in assertion (ii) have been derived by von Below (1988a). The $L^p$-estimates in assertion (i) follow similarly as in the proof of the theorem in von Below (1988a). The proof consists mainly of showing that the initial boundary value problems (A.6)–(A.7) are equivalent to a well-stated initial boundary value problem for a parabolic system, where the $L^p$-estimate results of Ladyzenskaja et al. (1968), Solonnikov (1965) for such a parabolic system can be applied. The details are omitted here. □

### A.3 Nonlinear Problem (IBVP)

This subsection is devoted to the existence, uniqueness, and positivity of solutions to the nonlinear problem **(IBVP)**. Assumptions **[H1]** and **[H2]** are assumed throughout this section.

We begin by introducing the definition of upper and lower solutions associated with problem **(IBVP)**.

**Definition A.5** A function $\overline{u} \in C^{2,1}(\Omega)$ is an upper solution of problem **(IBVP)** if $\overline{u}$ satisfies the following conditions

$$\begin{cases} \dfrac{\partial \overline{u}_j}{\partial t} - D_j \dfrac{\partial^2 \overline{u}_j}{\partial x_j^2} + v_j \dfrac{\partial \overline{u}_j}{\partial x_j} \geq f_j(x_j, \overline{u}_j)\overline{u}_j, & x_j \in (0, l_j),\ j \in I_{N-1},\ t \in (0, T), \\ \alpha_{j,1}\overline{u}_j(e_i, t) - \beta_{j,1}\dfrac{\partial \overline{u}_j}{\partial x_j}(e_i, t) \geq 0, & \forall e_i \in E_{\mathrm{u}},\ t \in (0, T), \\ \alpha_{j,2}\overline{u}_j(e_i, t) + \beta_{j,2}\dfrac{\partial \overline{u}_j}{\partial x_j}(e_i, t) \geq 0, & \forall e_i \in E_{\mathrm{d}},\ t \in (0, T), \\ \overline{u}_{i_1}(e_i, t) = \cdots = \overline{u}_{i_m}(e_i, t), & \forall e_i \in E_{\mathrm{r}},\ t \in (0, T), \\ \sum_{j=i_1}^{i_m} d_{ij} A_j D_j \frac{\partial \overline{u}_j}{\partial x_j}(e_i, t) \geq 0, & \forall e_i \in E_{\mathrm{r}},\ t \in (0, T), \\ \overline{u}_j(x_j, 0) \geq u_j^0(x_j), & x_j \in (0, l_j),\ \ j \in I_{N-1}. \end{cases} \tag{A.13}$$

A function $\underline{u}(x, t) \in C^{2,1}(\Omega)$ is a lower solution of problem **(IBVP)** if $\underline{u}$ satisfies the following conditions:

$$
\begin{cases}
\dfrac{\partial \underline{u}_j}{\partial t} - D_j \dfrac{\partial^2 \underline{u}_j}{\partial x_j^2} + v_j \dfrac{\partial \underline{u}_j}{\partial x_j} \le f_j(x_j, \underline{u}_j)\underline{u}_j, & x_j \in (0, l_j),\ j \in I_{N-1},\ t \in (0, T), \\
\alpha_{j,1}\underline{u}_j(e_i, t) - \beta_{j,1} \dfrac{\partial \underline{u}_j}{\partial x_j}(e_i, t) \le 0, & \forall e_i \in E_{\mathrm{u}},\ t \in (0, T), \\
\alpha_{j,2}\underline{u}_j(e_i, t) + \beta_{j,2} \dfrac{\partial \underline{u}_j}{\partial x_j}(e_i, t) \le 0, & \forall e_i \in E_{\mathrm{d}},\ t \in (0, T), \\
\underline{u}_{i_1}(e_i, t) = \cdots = \underline{u}_{i_m}(e_i, t), & \forall e_i \in E_{\mathrm{r}},\ t \in (0, T), \\
\sum_{j=i_1}^{i_m} d_{ij} A_j D_j \frac{\partial \underline{u}_j}{\partial x_j}(e_i, t) \le 0, & \forall e_i \in E_{\mathrm{r}},\ t \in (0, T), \\
\underline{u}_j(x_j, 0) \le u_j^0(x_j), & x_j \in (0, l_j),\ \ j \in I_{N-1}.
\end{cases}
\tag{A.14}
$$

According to the definition of upper and lower solutions, one can easily see the following result from Lemmas A.2 and A.3.

**Lemma A.6** *Assume that $\overline{u}$ and $\underline{u}$ are a pair of upper and lower solutions of problem* **(IBVP)** *and $\overline{u} \ge \underline{u}$ on $G \times \{0\}$. Then $\overline{u} \ge \underline{u}$ on $\Omega$. If additionally $\overline{u} \ge, \not\equiv \underline{u}$ on $G \times \{0\}$, then $\overline{u} > \underline{u}$ on $(G \backslash E_0) \times (0, T]$.*

With the aid of the above preliminaries, we are now able to state the main result of this subsection.

**Theorem A.7** *For any $u^0 \in L^p(G)$ $(p > 1)$ with $u^0 \ge 0$ a.e. in $G$, problem* **(IBVP)** *admits a unique classical solution $u$ for all $t > 0$, which satisfies $u \ge 0$ in $\Omega$. If additionally, $u^0 \not\equiv 0$, then $u(x, t) > 0$ for all $t > 0$ and $x \in G \backslash E_0$.*

***Proof*** Note that 0 and $M^* = \max\limits_{j \in I_{N-1}} \{M_j\}$ form a pair of upper and lower solutions to **(IBVP)**, where $M_j$'s are given in **[H2]**. Thus, in light of Theorem A.4 and Lemma A.6, the existence of a strong solution follows from the standard iterations of lower and upper solutions; the obtained solution is classical due to Theorem A.4 again. We omit the details of the proof here and refer interesting readers to Pao (1992) and Ye et al. (2011). The uniqueness and positivity of solutions are obvious consequences of Lemma A.6. The proof is thus complete. □

From now on, given $u^0 \in L^p(G)$ for some $p > 1$, denote by $u(x, t, u^0)$ the unique solution to problem **(IBVP)**. Clearly, we have

**Lemma A.8** *For any $\psi_1, \psi_2 \in L^p(G)$ with $\psi_1 \ge, \not\equiv \psi_2$ on $G$, $u(x, t, \psi_1) > u(x, t, \psi_2)$ for all $x \in G \backslash E_0$ and $t > 0$.*

We also have the following observation.

**Lemma A.9** *If* **[H3]** *is also satisfied, then for any $u^0 \in L^p$ with $u^0 \ge 0$ on $G$ and $\lambda \in (0, 1)$, $u(x, t, \lambda u^0) \ge \lambda u(x, t, u^0)$ on $G$ for all $t > 0$.*

***Proof*** For any $\lambda \in (0, 1)$, clearly $\lambda u(x, t, u^0)$ satisfies

$$\frac{\partial \lambda u_j}{\partial t} = D_j \frac{\partial^2 \lambda u_j}{\partial x_j^2} - v_j \frac{\partial \lambda u_j}{\partial x_j} + f_j(x_j, u_j)\lambda u_j,$$
$$\leq D_j \frac{\partial^2 \lambda u_j}{\partial x_j^2} - v_j \frac{\partial \lambda u_j}{\partial x_j} + f_j(x_j, \lambda u_j)\lambda u_j,\ x_j \in (0, l_j),\quad j \in I_{N-1},\ t > 0,$$

where we used assumption **[H3]**. It follows from Lemma A.6 that $\lambda u(x, t, u^0) \leq u(x, t, \lambda u^0)$ on $G$ for all $t > 0$. □

### A.4 Theory of Elliptic Equations

It is clear that Lemmas A.1 and A.2 imply the following strong maximum principle for elliptic equations and Hopf-type boundary lemma.

**Lemma A.10** *Assume that $c(x) \geq 0$ and is bounded from above on $G$. Let $u \in C(G) \cap C^2(G \backslash E_b)$ satisfy*

$$-D_j \frac{\partial^2 u_j}{\partial x_j^2} + v_j \frac{\partial u_j}{\partial x_j} + c_j(x_j)u_j \leq 0\ (\geq 0),\ \ x_j \in (0, l_j),\ \ j \in I_{N-1},$$

*and*

$$u_{i_1}(e_i) = \cdots = u_{i_m}(e_i),\ \ \sum_{j=i_1}^{i_m} d_{ij} A_j D_j \frac{\partial u_j}{\partial x_j}(e_i) \leq 0\ (\geq 0),\ \ \forall e_i \in E_r.$$

*Suppose that $u \leq M$ ($u \geq m$) on $G$ and $u(x_0) = M$ ($u(x_0) = m$) at some point $x_0 \in G \backslash E_b$. If $c(x) \not\equiv 0$, suppose that $M \geq 0$ ($m \leq 0$). Then*

$$u = M\ (u = m)\ \ \text{on } G.$$

**Lemma A.11** *Assume that $c(x) \geq 0$ and is bounded from above on $G$. Let $u \in C(G) \cap C^2(G \backslash E_b)$ satisfy*

$$-D_j \frac{\partial^2 u_j}{\partial x_j^2} + v_j \frac{\partial u_j}{\partial x_j} + c(x_j)u_j \leq 0\ \ (\geq 0),\ \ x_j \in (0, l_j),\ j \in I_{N-1}.$$

*Suppose that $u$ is continuously differentiable at some point $e_i \in E_b$, $u(e_i) = M$ ($u(e_i) = m$), and $u(x) < M$ ($> m$) for all $x \in G$. If $c \not\equiv 0$, assume that $M \geq 0$ ($m \leq 0$). Then $d_{ij} u_{x_j}(e_i) > 0$ ($< 0$).*

The following comparison principle immediately follows from Lemmas A.10 and A.11.

**Lemma A.12** *Assume that $c(x) \geq 0$ is bounded from above on $\Omega$ and $c_j\beta_{j,s} \not\equiv 0$ for some $j \in I_{N-1}$, $s \in \{1, 2\}$. Let $u \in C(G) \cap C^2(G\backslash E_{\mathrm{b}})$ satisfy*

$$\begin{cases} -D_j \dfrac{\partial^2 u_j}{\partial x_j^2} + v_j \dfrac{\partial u_j}{\partial x_j} + c_j(x_j)u_j \geq 0, & x_j \in (0, l_j),\ j \in I_{N-1}, \\ \alpha_{j,1}u_j(e_i) - \beta_{j,1}\dfrac{\partial u_j}{\partial x_j}(e_i) \geq 0, & \forall e_i \in E_{\mathrm{u}}, \\ \alpha_{j,2}u_j(e_i) + \beta_{j,2}\dfrac{\partial u_j}{\partial x_j}(e_i) \geq 0, & \forall e_i \in E_{\mathrm{d}}, \\ u_{i_1}(e_i) = \cdots = u_{i_m}(e_i),\ \sum_{j=i_1}^{i_m} d_{ij}A_jD_j\dfrac{\partial u_j}{\partial x_j}(e_i) \geq 0, & \forall e_i \in E_{\mathrm{r}}, \end{cases} \tag{A.15}$$

*and assume that $\frac{\partial u_j}{\partial x_j}(e_i)$ exists for $e_i \in E_{\mathrm{b}}$ if $\beta_{j,s} \neq 0$ for some $j \in I_{N-1}$, $s \in \{1, 2\}$. Then $u(x) \geq 0$ for all $x \in G$. If $u(x) \not\equiv 0$, then $u(x) > 0$ for all $x \in G\backslash E_0$.*

In what follows, we will establish the existence, uniqueness, and $L^p$ and Schauder estimates of solutions to the following linear elliptic problem:

$$\begin{cases} -D_j \dfrac{\partial^2 u_j}{\partial x_j^2} + v_j \dfrac{\partial u_j}{\partial x_j} + c_j(x_j)u_j = g_j(x_j), & x_j \in (0, l_j), \quad j \in I_{N-1}, \\ \alpha_{j,1}u_j(e_i) - \beta_{j,1}\dfrac{\partial u_j}{\partial x_j}(e_i) = 0, & \forall e_i \in E_{\mathrm{u}}, \\ \alpha_{j,2}u_j(e_i) + \beta_{j,2}\dfrac{\partial u_j}{\partial x_j}(e_i) = 0, & \forall e_i \in E_{\mathrm{d}}, \\ u_{i_1}(e_i) = \cdots = u_{i_m}(e_i),\ \sum_{j=i_1}^{i_m} d_{ij}A_jD_j\dfrac{\partial u_j}{\partial x_j}(e_i) = 0, & \forall e_i \in E_{\mathrm{r}}. \end{cases} \tag{A.16}$$

Indeed, by using the similar idea to that of von Below (1988a), we can write the boundary value problem on $G$ in (A.16) into an equivalent boundary value problem for an elliptic system and then obtain the following result about the existence and a priori estimates of solutions of (A.16).

**Theorem A.13** *The following assertions hold.*

(i) *Assume that $c$ is bounded on $G$ with $c(x) \geq, \not\equiv 0$ and $g \in L^p(G)$ $(p > 1)$, then* (A.16) *admits a unique strong solution $u \in W^2_p(G)$ and*

$$\|u\|_{W^2_p(G)} \leq C\|g\|_{L^p(G)},$$

*where the constant $C$ does not depend on $u$, $g$.*

(ii) *Assume that $c \in C^\alpha(G)$ with $c(x) \geq, \not\equiv 0$ and $g \in C^\alpha(G)$, then* (A.16) *admits a unique solution $u \in C^{2+\alpha}(G)$ and*

$$\|u\|_{C^{2+\alpha}(G)} \leq C\|g\|_{C^\alpha(G)},$$

*where the constant $C$ does not depend on $u$, $g$.*

Next, we develop the theory of upper and lower solutions to establish the existence and uniqueness of solution to the following nonlinear elliptic problem

$$\begin{cases} -D_j \dfrac{\partial^2 u_j}{\partial x_j^2} + v_j \dfrac{\partial u_j}{\partial x_j} = g_j(x_j, u_j), & x_j \in (0, l_j),\ j \in I_{N-1}, \\ \alpha_{j,1} u_j(e_i) - \beta_{j,1} \dfrac{\partial u_j}{\partial x_j}(e_i) = 0, & \forall e_i \in E_{\mathrm{u}}, \\ \alpha_{j,2} u_j(e_i) + \beta_{j,2} \dfrac{\partial u_j}{\partial x_j}(e_i) = 0, & \forall e_i \in E_{\mathrm{d}}, \\ u_{i_1}(e_i) = \cdots = u_{i_m}(e_i),\ \sum_{j=i_1}^{i_m} d_{ij} A_j D_j \dfrac{\partial u_j}{\partial x_j}(e_i) = 0, & \forall e_i \in E_{\mathrm{r}}. \end{cases} \tag{A.17}$$

**Definition A.14** A function $\overline{u} \in C^2(G)$ is an upper solution of (A.17) if $\overline{u}$ satisfies

$$\begin{cases} D_j \dfrac{\partial^2 \overline{u}_j}{\partial x_j^2} - v_j \dfrac{\partial \overline{u}_j}{\partial x_j} + g_j(x_j, \overline{u}_j) \le 0, & x_j \in (0, l_j),\ j \in I_{N-1}, \\ \alpha_{j,1} \overline{u}_j(e_i) - \beta_{j,1} \dfrac{\partial \overline{u}_j}{\partial x_j}(e_i) \ge 0, & \forall e_i \in E_{\mathrm{u}}, \\ \alpha_{j,2} \overline{u}_j(e_i) + \beta_{j,2} \dfrac{\partial \overline{u}_j}{\partial x_j}(e_i) \ge 0, & \forall e_i \in E_{\mathrm{d}}, \\ \overline{u}_{i_1}(e_i) = \cdots = \overline{u}_{i_m}(e_i),\ \sum_{j=i_1}^{i_m} d_{ij} A_j D_j \dfrac{\partial \overline{u}_j}{\partial x_j}(e_i) \ge 0, & \forall e_i \in E_{\mathrm{r}}. \end{cases} \tag{A.18}$$

A function $\underline{u}(x, t) \in C^2(G)$ is a lower solution of (A.17) if $\underline{u}$ satisfies

$$\begin{cases} D_j \dfrac{\partial^2 \underline{u}_j}{\partial x_j^2} - v_j \dfrac{\partial \underline{u}_j}{\partial x_j} + g_j(x_j, \underline{u}_j) \ge 0, & x_j \in (0, l_j),\ j \in I_{N-1}, \\ \alpha_{j,1} \underline{u}_j(e_i) - \beta_{j,1} \dfrac{\partial \underline{u}_j}{\partial x_j}(e_i) \le 0, & \forall e_i \in E_{\mathrm{u}}, \\ \alpha_{j,2} \underline{u}_j(e_i) + \beta_{j,2} \dfrac{\partial \underline{u}_j}{\partial x_j}(e_i) \le 0, & \forall e_i \in E_{\mathrm{d}}, \\ \underline{u}_{i_1}(e_i) = \cdots = \underline{u}_{i_m}(e_i),\ \sum_{j=i_1}^{i_m} d_{ij} A_j D_j \dfrac{\partial \underline{u}_j}{\partial x_j}(e_i) \le 0, & \forall e_i \in E_{\mathrm{r}}. \end{cases} \tag{A.19}$$

Based on Lemma A.12 and Theorem A.13, one can use the standard iterations of upper and lower solutions (see, for instance, Pao 1992; Ye et al. 2011) to conclude the following result.

**Theorem A.15** *Let $\overline{u}$ and $\underline{u}$ be a pair of upper and lower solutions of (A.17) satisfying $\overline{u} \ge \underline{u}$ on $G$ and $m = \min_G \underline{u} < M = \max_G \overline{u}$, and*

$$\begin{aligned} &|g_j(x_j, u_j) - g_j(y_j, v_j)| \\ &\quad \le K(|x_j - y_j|^{\alpha} + |u_j - v_j|),\ \forall (x_j, u_j),\ (y_j, v_j) \in G \times [m, M],\ j \in I_{N-1} \end{aligned}$$

*for some constants $K > 0$ and $\alpha \in (0, 1)$. Then* (A.17) *admits a solution $u \in C^{2+\alpha}(G)$ which satisfies $\underline{u} \le u \le \overline{u}$. Moreover,* (A.17) *admits a minimal solution $\tilde{w}$ and a maximal solution $\tilde{u}$ in $[\underline{u}, \overline{u}]$ in the sense that for any solution $w$ of* (A.17) *satisfying $\underline{u} \le w \le \overline{u}$, we have $\tilde{w} \le w \le \tilde{u}$.*

## Appendix B Proof of Proposition 3.1

Choose $\xi > 0$ large enough so that $f_j(\cdot, 0) - \xi < 0$ for all $j \in I_{N-1}$. For any $g \in X$, Theorem A.13 guarantees that the problem

$$\begin{cases} -D_j \dfrac{\partial^2 u_j}{\partial x_j^2} + v_j \dfrac{\partial u_j}{\partial x_j} + [\xi - f_j(\cdot, 0)]u_j = g_j(x_j), & x_j \in (0, l_j),\ j \in I_{N-1}, \\ \alpha_{j,1} u_j(e_i) - \beta_{j,1} \dfrac{\partial u_j}{\partial x_j}(e_i) = 0, & \forall e_i \in E_{\mathrm{u}}, \\ \alpha_{j,2} u_j(e_i) + \beta_{j,2} \dfrac{\partial u_j}{\partial x_j}(e_i) = 0, & \forall e_i \in E_{\mathrm{d}}, \\ u_{i_1}(e_i) = \cdots = u_{i_m}(e_i),\ \sum_{j=i_1}^{i_m} d_{ij} A_j D_j \dfrac{\partial u_j}{\partial x_j}(e_i) = 0, & \forall e_i \in E_{\mathrm{r}}, \end{cases} \tag{B.1}$$

has a unique solution $u$ satisfying

$$\|u\|_{C^{2+\alpha}(G)} \le C\|g\|_{C^\alpha(G)} \le C_1\|g\|_{C^1(G)}$$

for some constants $C > 0$ and $C_1 > 0$ independent of $u$ and $g$.

Define the operator

$$T : X \to X, \quad u = Tg. \tag{B.2}$$

Then $T$ is a linear and continuous operator that maps a bounded set in $X$ into a bounded set in $C^{2+\alpha}(G)$. Note that a bounded set in $C^{2+\alpha}(G)$ is a sequentially compact set in $X$. This implies that $T$ maps a bounded set in $X$ into a sequentially compact set in $X$. Hence, $T$ is a compact operator on $X$. Moreover, by Lemmas A.2 and A.3, $Tg \ge 0$ if $g \in X_+$, and $u = Tg \in X^o$. Therefore, $T$ is strongly positive. Let $r(T)$ be the spectral radius of $T$. It follows from the well-known Krein–Rutman theorem (see, for example, Du (2006), Theorem 1.2) that $r(T) > 0$ is a simple eigenvalue of $T$ with an eigenfunction $g^* \in X^0$, i.e., $Tg^* = r(T)g^*$, and there is no other eigenvalue of $T$ associated with positive eigenfunctions. Thus, $\psi^* = Tg^*$ satisfies $-\mathcal{L}\psi^* + \xi\psi^* = (1/r(T))\psi^*$ in $G$, and hence, $\lambda^* = \xi - 1/r(T)$ is a simple eigenvalue of (3.5) with positive eigenfunction $\psi^* \in X^o$ and no other eigenvalues of (3.5) correspond to positive eigenfunctions. Similarly as in the proof of Du (2006), Theorem 1.4, we can obtain that if $\lambda \ne \lambda^*$ is an eigenvalue of (3.5), then $Re(\lambda) \le \lambda^*$.

## Appendix C Proof of Theorem 3.3

We first prove (i). Case 1: $\lambda^* < 0$. Let $\psi^*$ be the eigenfunction of (3.5) associated with $\lambda^*$. For any $\phi \in X_+$, since $\psi^* \in X^o$, there exists $\sigma > 0$ such that $0 \leq \phi \leq \sigma\psi^*$ on $G$. Let $u(\cdot, t, \phi)$ be the solution of **(IBVP)** with initial condition $\phi$ and $\overline{u}(\cdot, t, \sigma\psi^*) = e^{\lambda^* t}\sigma\psi^*$ be the solution of (3.4) with initial condition $\sigma\psi^*$. By **[H1]**, we have

$$\frac{\partial \overline{u}_j}{\partial t} = D_j \frac{\partial^2 \overline{u}_j}{\partial x_j^2} - v_j \frac{\partial \overline{u}_j}{\partial x_j} + f_j(x_j, 0)\overline{u}_j \geq D_j \frac{\partial^2 \overline{u}_j}{\partial x_j^2} - v_j \frac{\partial \overline{u}_j}{\partial x_j} + f_j(x_j, \overline{u}_j)\overline{u}_j$$

for $x_j \in (0, l_j)$, $j \in I_{N-1}$, $t > 0$. Then

$$\begin{aligned} \frac{\partial u_j}{\partial t} \quad &- \left[ D_j \frac{\partial^2 u_j}{\partial x_j^2} - v_j \frac{\partial u_j}{\partial x_j} + f_j(x_j, u_j)u_j \right] = 0 \leq \frac{\partial \overline{u}_j}{\partial t} \\ &- \left[ D_j \frac{\partial^2 \overline{u}_j}{\partial x_j^2} - v_j \frac{\partial \overline{u}_j}{\partial x_j} + f_j(x_j, \overline{u}_j)\overline{u}_j \right] \end{aligned}$$

for $x_j \in (0, l_j)$, $j \in I_{N-1}$, $t > 0$. It follows from Lemma A.6 and the fact $0 \leq \phi \leq \sigma\psi^*$ that

$$0 \leq u(\cdot, t, \phi) \leq \overline{u}(\cdot, t, \sigma\psi^*)$$

for any $t \geq 0$. Therefore,

$$0 \leq \lim_{t\to\infty} u(\cdot, t, \phi) \leq \lim_{t\to\infty} \overline{u}(\cdot, t, \sigma\psi^*) \to 0 \ \text{ uniformly on } G,$$

which implies that $u \equiv 0$ is globally attractive for all initial conditions in $X_+$.
Case 2: $\lambda^* = 0$. For any $\phi \in X^o$, there exists some $\sigma_0 > 0$ such that $0 \leq \phi \leq \overline{u} := \sigma_0\psi^*$ and that $\overline{u}$ is an upper solution of (3.8). Let $u^{(1)}$ and $u^{(2)}$ be solutions of **(IBVP)** with initial conditions $\phi$ and $\overline{u}$, respectively. It follows from Lemma A.6 that $0 \leq u^{(1)}(x, t) \leq u^{(2)}(x, t) \leq \overline{u}(x)$. Note that $u^{(2)}$ is bounded and monotonically decreasing in $t$ by following the same proof of Ye et al. (2011), Lemma 3.2.4. Therefore, the similar proof of Ye et al. (2011), Lemma 3.2.5 shows that $\lim_{t\to\infty} u^{(2)}(\cdot, t) = V \geq 0$ and $V$ is a classical solution of (3.8). If $V(x) > 0$ at some $x \in G$, clearly $V \in X^o$. Then, by Proposition 3.2, we can easily obtain $\lambda^* > 0$, which gives rise to a contradiction. Hence, $V(x) \equiv 0$ on $G$. Therefore, $\lim\limits_{t\to\infty} u^{(1)}(x, t) = 0$. So we conclude that when $\lambda^* = 0$, $u \equiv 0$ is globally attractive for **(IBVP)** with respect to all initial conditions in $X_+$. Thus, (i) is proved.

We next prove (ii). Assume $\lambda^* > 0$. For sufficiently small $\epsilon > 0$, we have $f_j(x_j, \epsilon\psi_j^*) \geq f_j(x_j, 0) - \lambda^*$ for all $x_j \in (0, l_j)$, $j \in I_{N-1}$. This implies that $w_1 = \epsilon\psi^*$ is a lower solution of (3.8). Note that for any constant $K^* > \max\{M_1, \ldots, M_{N-1}\}$ where $M_j$'s are given in **[H2]**, $w_2(x) = K^*$ is an upper solution of (3.8). Let $\epsilon > 0$ be sufficiently small such that $w_2(x) \geq w_1(x) = \epsilon\psi^*(x)$ and $K^* > \min_{x\in G}\{\epsilon\psi^*(x)\}$. It follows from Theorem A.15 that (3.8) admits a positive solution $u^* \in X^o$.

Assume there are two distinct positive steady states of **(IBVP)**: $u_1^*$ and $u_2^*$. Since $K^*$ can be arbitrarily large and $\epsilon$ can be arbitrarily small, without loss of generality, assume that $u_1^*$ is the minimal solution of (3.8) and $u_2^*$ is the maximal solution of (3.8) in $[\epsilon\psi^*, K^*]$. Then $u_1^* \leq u_2^*$ on $G$. It suffices to show $u_1^* = u_2^*$. Suppose that $u_1^* \leq, \neq u_2^*$ on $G$. Recall that $u_1^*, u_2^* \in X^o$. By defining $\tau^0 = \sup\{\tau > 0 : \; u_1^* \geq \tau u_2^* \text{ on } G\}$, we then have $\tau^0 \in (0, 1)$ and $u_1^* \geq \tau^0 u_2^*$ on $G$. Due to **[H3]**, we further observe that $u_1^* \geq, \not\equiv \tau^0 u_2^*$. Thus, by Lemmas A.2, A.8, and A.9, we obtain

$$u_1^* = Q_t(u_1^*) \gg Q_t(\tau^0 u_2^*) \geq \tau^0 Q_t(u_2^*) = \tau^0 u_2^*, \; \forall t > 0,$$

where $Q_t$ is the solution map of **(IBVP)** defined as $Q_t(\psi) = u(x, t, \psi)$ for the solution $u(x, t, \psi)$ of **(IBVP)** with initial condition $\psi$. This implies that $u_1^*(x) - \tau^0 u_2^*(x) \in X^o$, which in turn implies that $u_1^*(x) - \tau^0 u_2^*(x) \geq \tau_0 u_2^*(x)$ on $G$ for some small $\tau_0 > 0$. This is a contradiction to the definition of $\tau^0$. Therefore, there is only a unique positive steady state $u^*$ of **(IBVP)**.

For any $u^0 \in X_+\backslash\{0\}$, the unique solution $u$ of **(IBVP)** satisfies that $u(\cdot, t) \in X^o$ for any $t > 0$. Thus, we can assume that $u^o \in X^o$. Then there exist some $\epsilon_0 > 0$ and $\sigma_0 \geq 1$ such that $\underline{u} = \epsilon_0 \psi^*$ and $\overline{u} = \sigma_0 K^*$ are lower and upper solutions of (3.8), respectively, and

$$\underline{u} = \epsilon_0 \psi^* \leq u^o \leq \sigma_0 K^* = \overline{u} \;\text{ on } G.$$

Let $u_1, u_2$ be solutions of **(IBVP)** with initial conditions $\underline{u}$ and $\overline{u}$, respectively. It follows from Lemma A.6 that $\underline{u}(x) \leq u_1(x, t) \leq u(x, t) \leq u_2(x, t) \leq \overline{u}(x)$. As before, it can be proved that $u_1$ and $u_2$ are monotonically increasing and decreasing in t, respectively (Ye et al. 2011, Lemma 3.2.4). Therefore, $u_1$ and $u_2$ are bounded and monotonic with respect to $t$. Additionally, we can claim $\lim_{t\to\infty} u_1(\cdot, t) = U$ and $\lim_{t\to\infty} u_2(\cdot, t) = V$. Furthermore, we can prove $U$ and $V$ are solutions of (3.8) [see Lemma 3.2.5 in Ye et al. (2011)]. Then $\underline{u}(x) \leq U(x) \leq V(x) \leq \overline{u}(x)$. Hence, $U(x) = V(x) = u^*$, and $\lim_{t\to\infty} u(x, t) = u^*(x)$. Therefore, we have proved that $u^*$ is globally attractive with respect to any initial values in $X_+\backslash\{0\}$.

## Appendix D The Hydraulic Relation in a Gradually Varying Flow

The hydraulic relation in a gradually varying flow can be found in, e.g., Chaudhry (1993). For self-completeness of this paper, we briefly provide the relation as below. The governing equation for the gradually varying flow is given by

$$\frac{\mathrm{d}y}{\mathrm{d}x} = \frac{S_0(x) - S_f(y)}{1 - F_r^2(y)} \tag{D.1}$$

(see (5–7) in Chaudhry 1993), where $x$ (unit: m) represents the longitudinal location along the river, $y(x)$ (unit: m) is the water depth at location $x$, $S_0(x)$ is the slope of the channel bed at location $x$, $S_f$ is the friction slope, i.e., the slope of the energy grade line, and $F_r$ is the Froude number that is defined as the ratio between the flow velocity and the water wave propagation velocity. In the case where the river has a rectangular cross section with a constant width $B$ (unit: m) and a constant bed slope $S_0$, the water depth $y(x)$ is stabilized at the normal depth

$$y_n = \left( \frac{Q^2 n^2}{B^2 S_0 k^2} \right)^{\frac{3}{10}}, \tag{D.2}$$

where $Q$ (unit: $\mathrm{m}^3$/s) is the flow discharge, $k = 1$ is a dimensionless conversion factor, and $n$ (unit: s/$\mathrm{m}^{1/3}$) is Manning's roughness coefficient, which represents the resistance to water flows in channels and depends on factors such as the bed roughness and sinuosity. The flow in such a river is called a uniform flow.

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