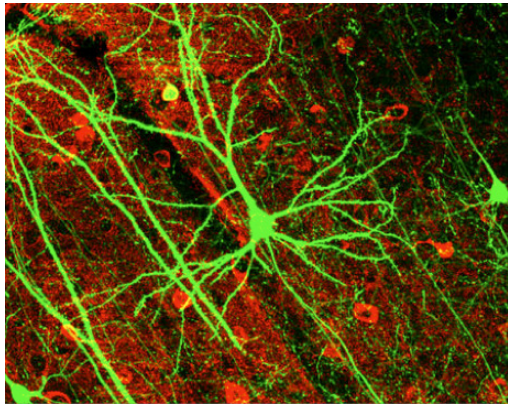# Extending Dynamics to Tree Graph Domains: Two Examples from Math Biology
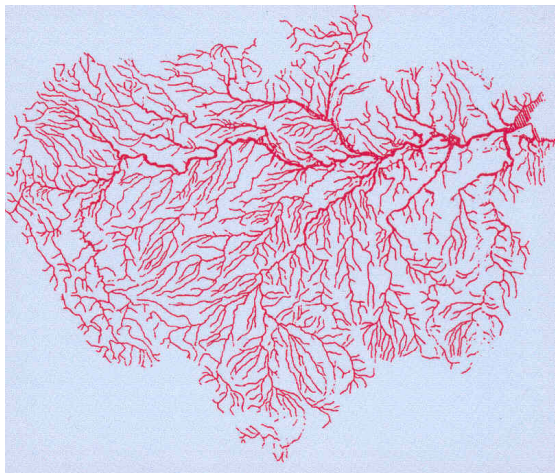
Jon Bell, UMBC
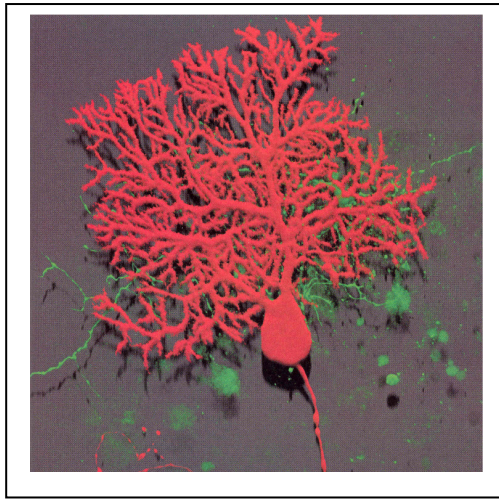
1. Cable theory and dendritic trees

(Pyramidal cell from mouse cortex; by Santiago Ramon)

2. Population persistence in advection-dominated environments (river networks)
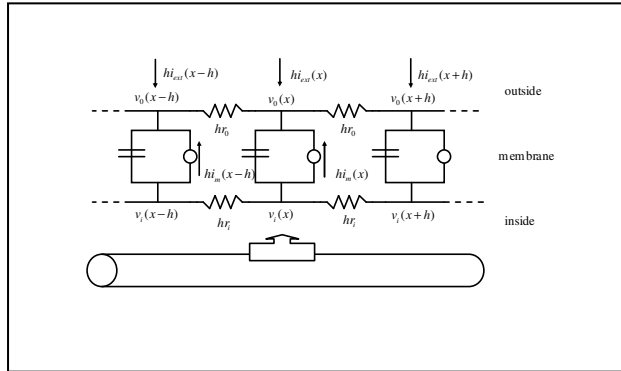
(Amazon river basin: courtesy of Hideki Takayusu)

(Purkinje cells, fluorenscent dyed;

Technology Review, Dec. 2009)
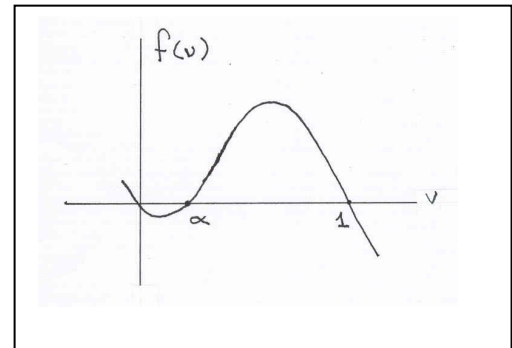
$$\frac{a}{2R_i}\frac{\partial^2 v}{\partial x^2} = C_m \frac{\partial v}{\partial t} + I_{ion}(v,\ldots) = C_m \frac{\partial v}{\partial t} + \begin{cases} \displaystyle\sum_{ion-j} g_j(\underline{w})(v - E_j) \\[2ex] \displaystyle\frac{v}{R_m} \end{cases}$$

Example dynamics for this talk: bistable equation

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + f(u)$$

$$H_f := \begin{cases} f \in C^1[0,A] & A > 1 \\ f(0) = f(1) = 0 \\ \quad f(v) < 0 & for \quad 0 < v < \alpha \\ \quad f(v) > 0 & for \quad \alpha < v < 1 \\ \displaystyle\int_0^1 f(s)\,ds > 0 \end{cases}$$

$$\Omega = E \cup V$$

$$E = \{e_1, e_2, ..., e_N\}, V = \{v_1, v_2, ..., v_M\}$$

$$\partial\Omega = \{v \in V \mid index(v) = 1\} = \{\gamma_1, \gamma_2, ..., \gamma_m\}$$

$$V \setminus \partial\Omega = \{v \in V \mid index(v) > 2\}$$

Ω = metric graph if every edge $e_j \in E$ is identified with an interval of the real line with positive length ℓ_j.

Ω = tree graph if there are no cycles.

Problem:

(1) $\dfrac{\partial u}{\partial t} = \dfrac{\partial^2 u}{\partial x^2} + f(u)$ on $\{\Omega \setminus V\} \times (0, T)$

(2) $u = 0$ on $\Omega \times \{0\}$

(3) $\displaystyle\sum_{e_j \sim v} \partial u_j(v, t) = 0$ for $v \in V \setminus \{\gamma_1\}$ (Kirchhoff-Neumann)

u is continuous at v

(4) $-\partial u_1(\gamma_1, t) = I(t) > 0$ for $t \in [0, T]$

H_{f1}: There exists $u_0, f_0 > 0$ such that for $0 \le u \le u_0$, $f(u) \le -f_0 u$.

Let $Z^T := C(\Omega \times [0, T]) \cap C^{2,1}(\{\Omega \setminus V\} \times (0, T])$.

Theorem: Let f satisfy H_f, H_{f1}. Let $u \in Z^T$ be a solution to (1)-(4), for any T > 0, where $I(t) = \begin{cases} I_0 & for \quad 0 < t < t_0 \\ I_1 e^{-\delta(t - t_0)} & for \quad t \ge t_0 \end{cases}$. Here $I_0 \ge I_1 > 0, \quad 0 < \delta < f_0$. Then

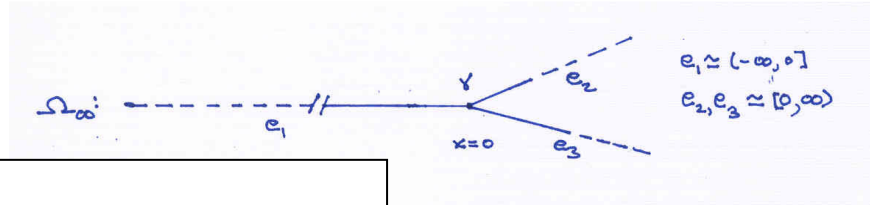$\displaystyle\lim_{t \to \infty} u_j(x, t) = 0$ for all $x \in e_j$, all $j = 1, ..., N$.

H_{f2}: for some $f_b > 0$, $f(u) \ge -f_b u$ for $u \ge 0$.

Theorem: Let f satisfy H_f, H_{f1}. Let $u \in Z_T$ solve (1)-(4) with $I(t)$ replaced by $\mu I^*(t)$, where $I^*(t) \ge 0$, I^* not identically zero. Then there exists a μ_0 depending on I^*, such that if $\mu > \mu_0$, for each j, $u_j(x, t) \ge v_j(x, t)$ and

$\displaystyle\lim_{t \to \infty} v_j(x, t) = 1$.

Bounds on the Speed of Propagation: IVP example

Consider the problem in $\Omega_\infty \times (0,\infty)$:

(IVP) =

$$
\begin{cases}
u_t = u_{xx} + f(u) & in \quad \{\Omega \setminus V\} \times (0,T) \\
\quad u = \phi & in \quad \Omega \times \{0\} \\
KN + continuity \quad at : \gamma & t > 0
\end{cases}
$$

Assume u is a solution to (IVP) such that
(*) $\lim\limits_{t\to\infty} u_j = 1$ in $\Omega_\infty \times (0,\infty)$

Write $f(u) = f'(0)u + g(u) = -au + g(u)$, g is smooth, $g(u) = O(u^2)$ as
$u \to 0$. Define $\sigma := \sup\limits_{0<u<1}\{g(u)/u\} > 0$.

Note that $\mathcal{L}u_j := u_{jt} - u_{jxx} + au_j - \sigma u_j = g(u_j) - \sigma u_j \le 0$.

Assume $0 \le \phi_j \le 1$, $j = 1,2,3$. Then (by another comparison result),
$0 \le v_j \le 1$.

Theorem: Suppose v is a solution to (IVP) satisfying (*). Let ϕ have
bounded support, $\operatorname{supp}\phi \subset e_1$. If $c > \bar{c} := 2\sigma/\sqrt{a+\sigma}$, then for each j, each
$x \in e_j$, $\lim\limits_{t\to\infty} u_j(x+ct,t) = 0$.

Suppose (IVP) admits a positive steady state solution $q(x)$ for
$a \le x \le b < 0$, with $q(a) = q(b) = 0$. Suppose the only nonnegative global
steady state τ of (IVP) with $\tau_1(x) \ge q(x)$ on $[a,b]$ is $\tau \equiv 1$. Let u be a
solution to (IVP) with $\phi_1(x) \ge q(x)$ on $[a,b]$.
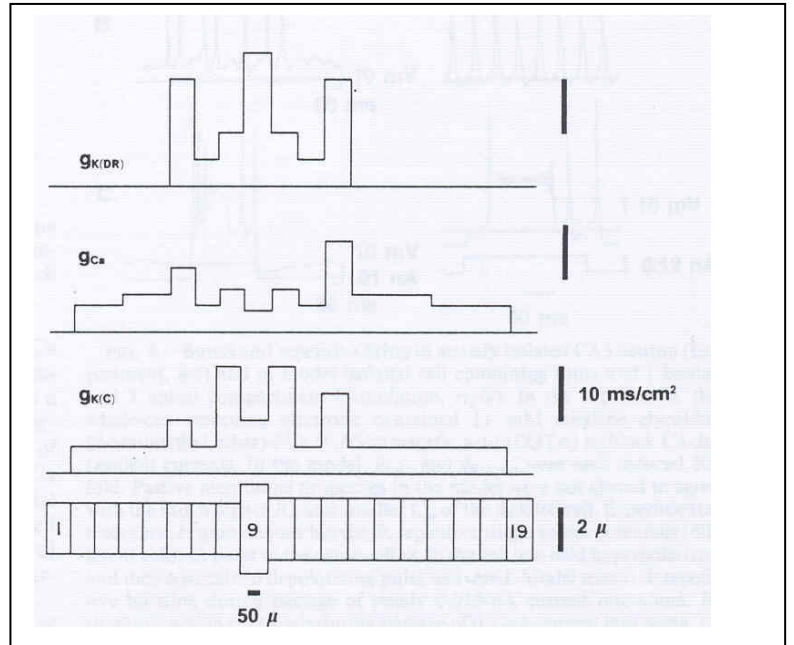
Then there is a $\underline{c} > 0$ such that for $0 < c < \underline{c}$, for any x, any $\varepsilon > 0$, there
is a $T > 0$ such that for $t > T$, $u_j(x+ct,t) \ge 1 - \varepsilon$, $j = 1,2,3$.

Inverse Problem

Motivation:
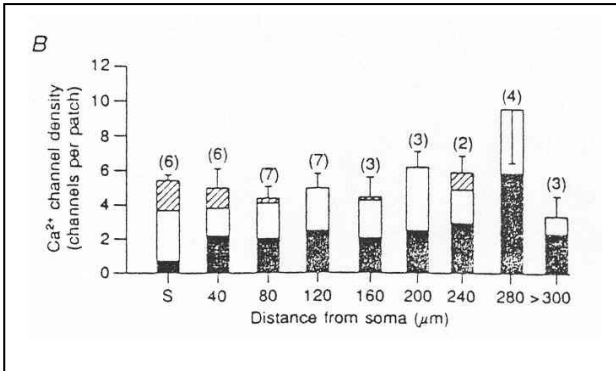
Problem: (1) $\quad u_t + q(x)u = u_{xx}$ on $\{\Omega \setminus V\} \times (0,T)$

(2) $\quad u = 0$ $\qquad$ on $\Omega \times \{0\}$

(3) $\quad \sum_{e_j \sim v} \partial u_j(v,t) = 0$ $\quad$ for $v \in V \setminus \partial\Omega$

$\qquad u$ is continuous at $v \in V \setminus \partial\Omega$

(4) $\quad \partial u = f \in L^2([0,T], \Re^m)$ on $\partial\Omega \times [0,T]$

Strategy: determine *q(x)* on boundary edges via Boundary Control Theory, then "prune" tree to smaller tree.

Reference: Avdonin & Bell, JMB, 2012; Avdonin & Bell, submitted, Inverse Problems

Another Problem: $(1 + q(x))u_t + q(x)u = u_{xx}$

Some Questions/Remarks

Subprojects:

1. Tree with variable edge diameters: **conduction block**

Let $u = \varphi$ on $\Omega_\infty \times \{0\}$, so $u(x,t;\varphi)$ is a solution on $\Omega_\infty \times (0,T]$. For a class $\mathcal{A}$ of admissible i.c.s, let $\psi_1, \psi_2 : \Omega_\infty \to \Re$ have property that $\psi_1 \le u(\cdot,t;\varphi) \le \psi_2$ in $\Omega_\infty \times [0,T]$. Then $\{\psi_1,\psi_2\}$ will be a trap for $\mathcal{A}$. $u(x,t;\varphi)$ will be blocked at γ if there is a trap $\{\psi_1,\psi_2\}$ such that $\|\psi_i\| \le \rho(\varepsilon)$, $i = 1,2$ and $\rho(\varepsilon) \to 0$ as $\varepsilon \to 0+$.

2. Distal current sources: Given stimulus $I(t)$, voltage boundary conditions on $\partial\Omega \setminus \{\gamma_1\}$, and sealed-end conditions, can we estimate u_1 at γ_1 (representing potential at the soma)?

3. We have (weak) threshold conditions for FHN system on $\Omega \times (0,\infty)$:

$$u_t = u_{xx} + f(u) - w, \quad w_t = \sigma u - \mu w$$

4. Want to show existence of a traveling wave solution on $\Omega_\infty \times (0,T]$.

5. Want to explore (numerically) other properties, e.g., wave attenuation and amplification along graph domains.

Mediterranean Sea — Early Sites of the Delta
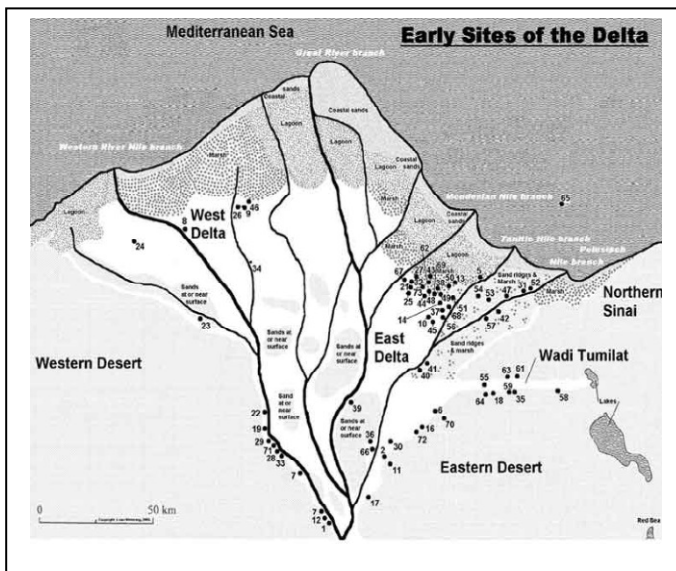
Population Persistence
in River Networks
(metric tree graph)

Query: How do populations persist in face of downstream biased flow? (The "drift paradox"; Muller, 1954; Hershey, et al, 1993, …)

Suggestions: drifting populations represent a surplus that would not otherwise contribute to local persistence, or compensatory upstream movements (colonization cycle).

Lutscher, et al, 2010: populations must have ability to invade upstream in order to persist.

Usual modeling: involves an advection-diffusion-reaction equation on a finite interval (single river branch), or on the real line.

References above initiated persistence investigations on a branching (metric graph) domain.

(1) $u_t = Du_{xx} - su_x + f(u)$ in $\{\Omega \backslash V\} \times (0, \infty)$

u = population density s = downstream advection speed (population

drift), which may differ from rate of current

due to organism behavior

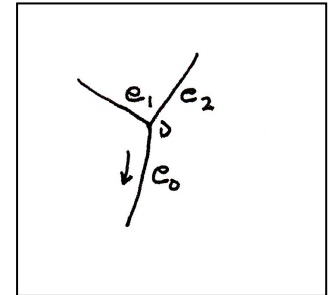$f(u)$ = birth/death process. Here let $f(u) = ru, \quad r > 0$

Flux on $e_j = q_j(\cdot, t) = A_j \left(-D_j \dfrac{\partial u_j}{\partial x} + s_j u_j \right)$, A_j = cross-sectional area of segment

Simplifying model assumptions: $D_j = D, \quad s_j = s, \quad all\_j$

x increases downstream

Continuity at vertex V: $u_0 = u_1 = u_2, \quad t \geq 0$

Conservation at vertex V: $q_0(V, t) = q_1(V, t) + q_2(V, t)$

At interior vertex V, incident sectional area difference is $B_V = A_0 - A_1 - A_2$.

Assume

(2) $B_V s = (A_0 - A_1 - A_2)s \geq 0$ for $V \in V \backslash \partial \Omega$

Upstream boundary vertex condition: $q(\gamma, t) = 0, \quad \gamma \in \partial \Omega$

Inhospitable river ending at downstream vertex γ_d: $u(\gamma_d, t) = 0$

Reduction: $u(x,t) = e^{sx/2D} w(x,t) \Rightarrow$

(3) $\quad w_t = Dw_{xx} + (r - \dfrac{s^2}{4D})w = 0$ in $\{\Omega \setminus V\} \times (0,\infty)$

(4) at $\gamma \in \partial\Omega \setminus \{\gamma_d\}$: $q = A_j\left(D\dfrac{\partial w}{\partial x} - \dfrac{s}{2}w\right) = 0$ $\quad (e_j \sim \gamma)$

(5) at γ_d : $w(\gamma_d, t) = 0$

(6) at $v \in V \setminus \partial\Omega$: $A_0\left(\dfrac{s}{2}w_0 - D\dfrac{\partial w_0}{\partial x}\right) = A_1\left(\dfrac{s}{2}w_1 - D\dfrac{\partial w_1}{\partial x}\right) + A_2\left(\dfrac{s}{2}w_2 - D\dfrac{\partial w_2}{\partial x}\right)$

Remark: On $\Omega \setminus V$, set $r - s^2/4D = 0$, $L := D\dfrac{\partial^2}{\partial x^2} \Rightarrow w_t = Lw$ is formally self-adjoint. With Ω a metric tree graph with finitely many edges, L can be shown self-adjoint with compact resolvent, so there is a spectrum $\{\lambda_j\}$, $\lambda_j \to -\infty$; and an ON basis $\{\varphi_j\}$ of eigenfunctions. When

(2) $\quad B_v s = (A_0 - A_1 - A_2)s \geq 0$ at each $v \in V \setminus \partial\Omega$

w equation satisfies a maximum principle. If $u(x,t)$ on Ω is continuous, non-negative, then $u(x,t) \geq 0$ for all $t > 0$.

Theorem: Suppose w satisfies (3)-(6), with (2) holding. Then, if $r - s^2/4D < |\lambda_1|$, the population will not persist. (In particular, it will not persist if $r - s^2/4D \leq 0$.) If $r - s^2/4D \geq |\lambda_1|$ a continuous positive initial population will persist.

1. For the **linear** advection-diffusion-reaction equation on a finite interval , with no flux at $x=0$, homogeneous Dirichlet condition (hostile river ending) at $x=L$, it is an undergraduate exercise to show no persistence (i.e., population decreases) if $r-s^2/4D \leq -\lambda_1$ (and growth if $r-s^2/4D > -\lambda_1$).

2. On a single branch, with

$$u_t = Du_{xx} - su_x + ru(1-u) \quad \text{on} \quad 0 < x < L, \quad t > 0$$

$$(-Du_x + su)(0,t) = 0, \quad u_x(L,t) = 0, \quad t > 0$$

Vasilyeva & Lutscher, 2012 show there is no positive steady state if $r-s^2/4D \leq 0$ (no persistence). For each D,s and $r-s^2/4D > 0$ there exists a $L^* = L^*(D,s)$ such that there is a unique positive steady state if $L > L^*$, and it is stable. We are pushing the Vasilyeva-Lutscher work to the metric tree graph setting, using

$$f(u) = ru(1-u)(u-\alpha)$$

Which encompasses an allee-type mechanism.

3. Further out in consideration is to explore competition in a network advection-driven environment; maybe with basic equations

$$\begin{cases} u_t = D_1 u_{xx} - su_x + u(1-u-av) \\ v_t = D_2 v_{xx} - sv_x + v(r-v-bu) \end{cases}$$

4. Return to a single population, but consider parameters that vary depending on branch, and investigate different downstream river ending boundary conditions.
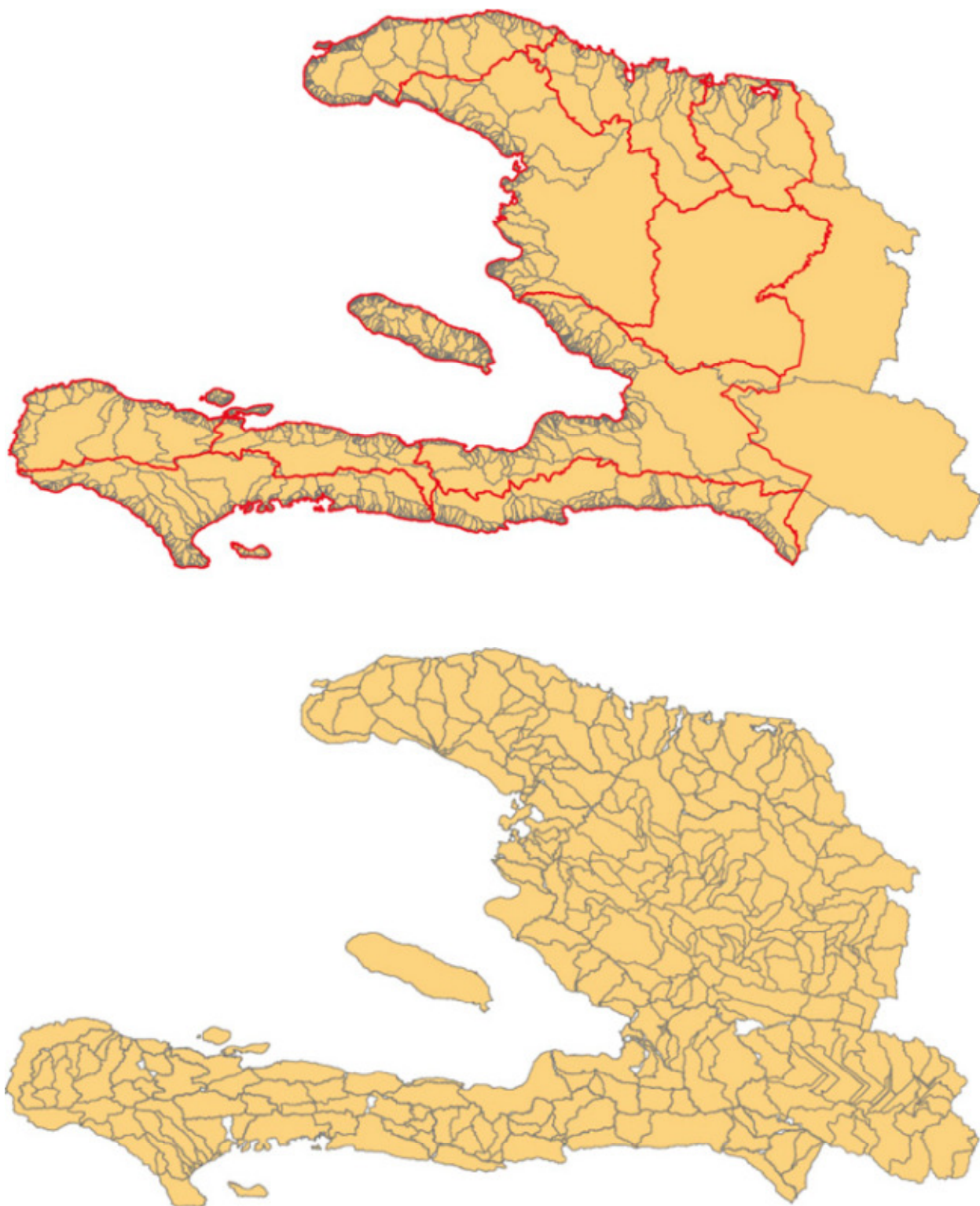
From A. Rinaldo, et al, PNAS, 109(17), 2012.

Landolfa, Barth, 1996; Eberhard, Chacon, 1980:

Webs are an extension of the spider's sensory space, as well as a mechanical device for prey interception and retention. The spider must solve two problems with the web, namely discrimination of and orientation towards detected sources. How does the web structure affect sensitivity and directional transmission?
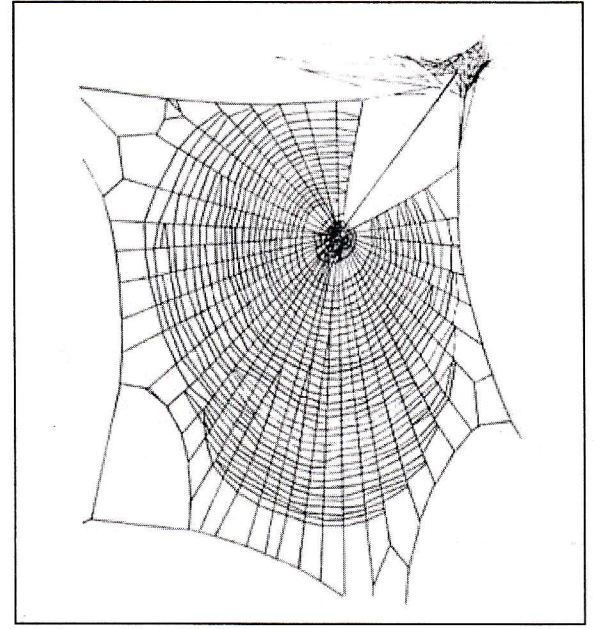
Honeycombs are examples of <u>ramified spaces</u>

Sandeman, et al, 1996:

Vibration of the rims of open honeycomb cells is transmitted across the comb. Honeybees have receptors on their legs for detecting vibrations in the range emitted by a bee during its dance. Framed (commercial) combs strongly attenuate higher frequencies, whereas these frequencies are amplified in small, open (natural) combs. Bees have a habit of freeing an area of comb from the frame in those areas used for dancing.