A convenient form of complexity in ecology: multiple timescales

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Case 1: Aphids and Ladybugs on Patches

Aphids:
- Many generation per summer
- Aphids mostly stay on one patch of plants, move short distances randomly

Ladybugs:
- One generation per summer
- Ladybugs move distances up to a kilometer, aggregate where there might be aphids
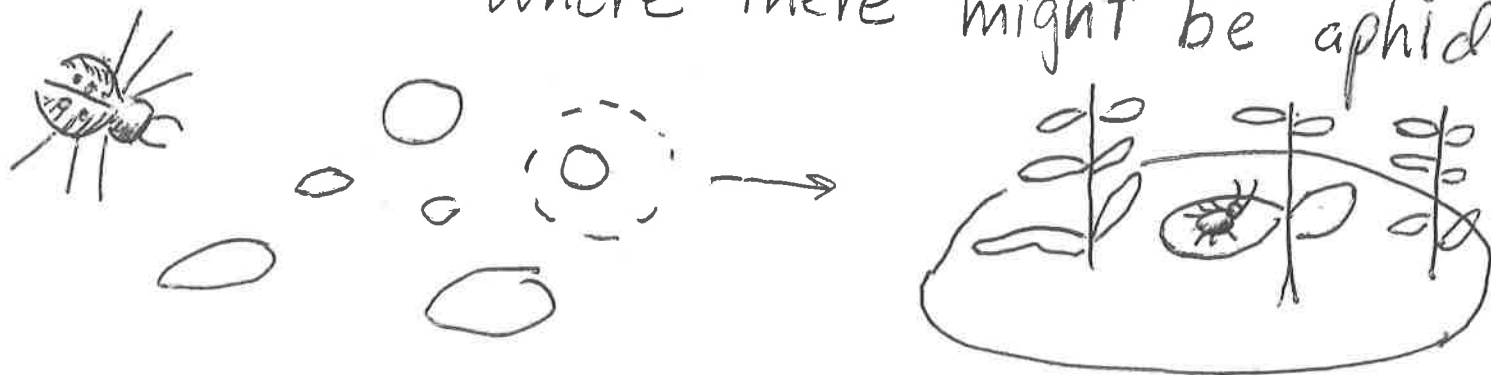
Motivating Question:

In a classical diffusive model

$$\frac{\partial v}{\partial t} = D\Delta v + R\left(1 - \frac{v}{K}\right)v \quad \text{on } \Omega$$

$$v = 0 \quad \text{on } \partial\Omega,$$

population density increases with patch size.

Observation: • As aphids recolonized a cleared area where patches of plants had regrown, this pattern held true in the first year.

• In later years it did not.

$\Rightarrow$ Could recolonization by Ladybugs cause that?

A model:

Patches Ω_n in $\mathbb{R}^2$, $n = 1, \ldots, N$

v_n = aphid density in patch n

(assume $v_n(x, 0) \geq 0, \not\equiv 0$, on Ω_n)

Overall Region

Patches Ω_n

$A_n = |\Omega_n|$

ℓ = total Ladybug population in region

ℓ_n = # of Ladybugs on Ω_n

$\ell_A = \ell - \sum_{n=1}^{N} \ell_n$ = # of Ladybugs in air

$$\frac{\partial v_n}{\partial t} = D \Delta v_n + R\left(1 - \frac{v_n}{K}\right)v_n - c \frac{\ell_n}{A_n} v_n \quad \text{in } \Omega_n$$

days

$v_n = 0$ on $\partial \Omega_n$

minutes $\frac{d\ell_n}{d\tau}$
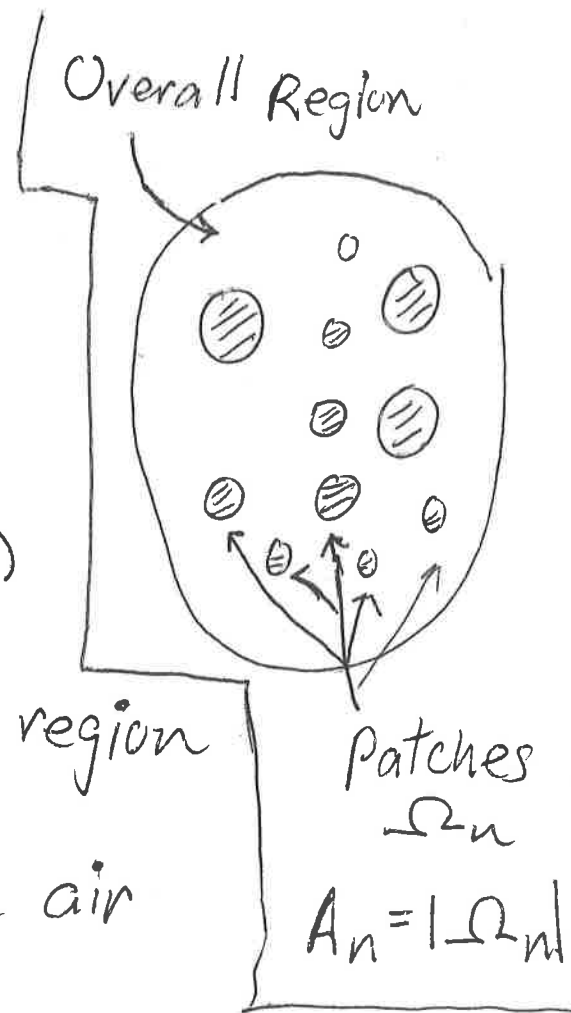
$$\frac{d\ell_n}{dt} = I_n \ell_A - E_n \ell_n = I_n\left(\ell - \sum_{m=1}^{N} \ell_m\right) - E_n \ell_n$$

immigration   emigration

Fast timescale τ: Assume $p_n \to$ equilibrium p_n^*

$$0 = I_n \left(p - \sum_{m=1}^{N} p_m \right) - E_n p_n \qquad n = 1, \ldots, N$$

(sum over n, solve for $\sum_{n=1}^{N} p_n$, substitute back.)

$$p_n^* = \frac{(I_n / E_n)\, p}{1 + \sum_{m=1}^{N} (I_m / E_m)}$$

(Note: we could allow $p = p(t)$, but did not.)

Options for I_n and E_n include $I_n = i\, A_n^p$, $E_n = \dfrac{e}{A_n^q \, \overline{V}_n(t)^r}$

where $A_n = |\Omega_n|$, $V_n = \int_{\Omega_n} V_n(x,t)\, dx$, (i and e constants, also p, q, r, all > 0)

(This captures predator aggregation (concentration) on patches with higher prey densities)

Slow Timescale

← predator density

$$\frac{\partial V_n}{\partial t} = D \Delta V_n + R\left(1 - \frac{V_n}{K}\right) V_n - c \frac{P_n}{A_n} V_n \quad \text{on } \Omega_n,$$

$$V_n = 0 \quad \text{on } \partial \Omega_n, \quad n = 1, \ldots, N$$

$$\boxed{\begin{array}{l} A_n = |\Omega_n| \\ \bar{V}_n = \int_{\Omega_n} V_n \, dx \end{array}}$$

with

$$P_n = P_n^* = \frac{(I_n/E_n) P}{1 + \sum_{m=1}^{N} (I_m/E_m)} = \frac{(i/e) A_n^{p+q} \bar{V}_n^r P}{1 + (i/e) \sum_{m=1}^{N} A_m^{p+q} \bar{V}_m^r}$$

so

$$\frac{\partial V_n}{\partial t} = D \Delta V_n + R\left(1 - \frac{V_n}{K}\right) V_n - c \frac{(i/e) A_n^{p+q} (P/A_n) \bar{V}_n^r V_n}{1 + (i/e) \sum_{m=1}^{N} A_m^{p+q} \bar{V}_m^r}$$

(**Cooperative** system: if $V_m \uparrow$ then $\bar{V}_m \uparrow$

so if $\bar{V}_m \uparrow$ for $m \neq n$ then $\partial V_n / \partial t \uparrow$.) $\quad$ ($\bar{V}_m$ constant in x)

Application - Effects of patch size on aphid population

At equilibrium $v_n = v_n^*$ satisfying

$$0 = D \Delta v_n^* + R\left(1 - \frac{v_n^*}{K}\right)v_n^* - C\, v_n^* \text{ in } \Omega_n, \quad v_n^* = 0 \text{ on } \partial\Omega_n$$

C = constant, depending on $V_1, \ldots, V_N$ and $A_1, \ldots, A_N$

but
$$0 = D\Delta\theta + (a - b\theta)\theta \text{ in } \Omega, \quad a, b \text{ constant}$$
$$\theta = 0 \text{ on } \partial\Omega$$

is well understood - so analysis is still
sometimes possible.

If we assume large scale aggregation of
Ladybugs - so $\ell = \ell_0\left(\sum\limits_{n=1}^{N} A_n\right) = \ell_0 \text{(total patch area)}$
then for some parameter ranges we get
(Patch 1 largest)

$V_1^* = \int_{\Omega_1} v_1^*$

Case 2: Evolution of dispersal

Time / space scales: (medium-large mammals)

1) Random walk, step by step
   (seconds - minutes / meters)

2) Population level dispersal (diffusion, advection)
   (hours - days / kilometers)

3) Population interactions and dynamics
   (weeks - years / species ranges
                    (up to hundreds of kilometers)

4) Evolution of dispersal
   (thousands of years / species ranges)

Random walks $\longrightarrow$ Population level dispersal

Diffusion limit
$(k=0,1,2)$

$x-\Delta x \qquad x \qquad x+\Delta x$

$$\frac{(\Delta x)^2}{\Delta t} = C, \quad D_k(x) = C p_k(x)$$

At each time step Δt,
move one space step Δx

Let $\Delta x, \Delta t \longrightarrow 0$

$p(x,t) = $ continuous PDF
for limit

Cases:

PDE form for p:

$(0) \quad \ell(x|x-\Delta x) = \ell(x+\Delta x, x) = p_0(x) \longrightarrow \dfrac{\partial p}{\partial t} = \dfrac{\partial}{\partial x}\left(D_0(x)\dfrac{\partial p}{\partial x}\right)$

$(1) \quad \begin{cases} \ell(x|x-\Delta x) = p_1(x-\Delta x) \quad \left(\begin{array}{c}\text{departure}\\ \text{point}\end{array}\right) \\ \ell(x+\Delta x, x) = p_1(x) \end{cases} \longrightarrow \dfrac{\partial p}{\partial t} = \dfrac{\partial^2}{\partial x^2}\left(D_1(x)p\right)$

$(2) \quad \begin{cases} \ell(x|x-\Delta x) = p_2(x) \quad \left(\begin{array}{c}\text{arrival}\\ \text{point}\end{array}\right) \\ \ell(x+\Delta x| x) = p_2(x+\Delta x) \end{cases} \longrightarrow \dfrac{\partial p}{\partial t} = \dfrac{\partial}{\partial x}\left(D_2^2(x)\dfrac{\partial}{\partial x}\left(\dfrac{p}{D_2(x)}\right)\right)$

Random walk $\longrightarrow$ Population dispersal

vs.

Population dispersal $\longrightarrow$ equilibrium distribution
(closed environment)
(no-flux b.c.)

Cases again:

$$t \longrightarrow \infty$$

(0) $\quad \dfrac{\partial p}{\partial t} = \dfrac{\partial}{\partial x}\left(D_0(x)\dfrac{\partial p}{\partial x} \right) \qquad p(x,t) \longrightarrow C$

(1) $\quad \dfrac{\partial p}{\partial t} = \dfrac{\partial^2}{\partial x^2}\left(D_1(x)p \right) \qquad p(x,t) \longrightarrow C/D_1(x)$

(2) $\quad \dfrac{\partial p}{\partial t} = \dfrac{\partial}{\partial x}\left(D_2^2(x)\dfrac{\partial}{\partial x}\left(\dfrac{p}{D_2(x)} \right) \right) \qquad p(x,t) \longrightarrow C D_2(x)$

The form of random walk (scale $\Delta x, \Delta t$)
determines the possible patterns arising from dispersal
(scale x, t)

Population level models (movement)

(timescale t)

$u(x, t, T)$ = population density

$t \sim$ movement
$T \sim$ population dynamics

"Classical" models: $t = T$

$$\frac{\partial u}{\partial t} = \nabla \cdot [\mu(x) \nabla u - u \vec{P}(x)] + f(x, u)$$

but timescales suggest we look at

$$\frac{\partial u}{\partial t} = \nabla \cdot [\mu(x) \nabla u - u \vec{P}(x)], \text{ let } t \to \infty; \text{ then}$$

we expect $u \to \phi(x) U(T)$

$$\nabla \cdot [\mu \nabla \phi - \phi \vec{P}] = 0 \quad \bigstar$$

Then look for $U(t)$

$$\frac{\partial U}{\partial T} = F(U) = ??$$

$\bigstar$ The assumptions on movement in the $(\Delta x, \Delta t)$ scale constrain possible forms of ϕ

Population level models $\left(\begin{array}{c}\text{dynamics}\\\text{timescale } T\end{array}\right)$

· logistic case: L = dispersal operator

ϕ = principal eigenfunction of L

$$u(x,t,T) \to \phi(x)\, U(T)$$

$$f(x,u) = (m(x)-u)u \qquad (\text{so } L\phi = 0)$$

$$\phi(x)\frac{dU}{dt} = \underbrace{(L\phi)U}_{=0} + \big[m(x) - \phi(x)\,U(T)\big]\,\phi(x)\,U(T) \qquad \boxed{\begin{array}{l}\text{Later normalize}\\ \left(\int_\Omega \phi\, dx = 1\right)\end{array}}$$

Integrate x, $\div$ by $\int_\Omega \phi(x)\,dx$

$$\frac{dU}{dt} = \left(\frac{\int_\Omega m(x)\,\phi(x)\,dx}{\int_\Omega \phi(x)\,dx}\right) U(T) - \left(\frac{\int_\Omega \phi(x)^2\,dx}{\int_\Omega \phi(x)\,dx}\right) U(T)^2$$

Let $\bar{u} = \dfrac{U(T)}{|\Omega|}$, $\bar{\phi} = \dfrac{\int_\Omega \phi(x)\,dx}{|\Omega|}$, $\bar{m} = \dfrac{\int_\Omega m(x)\,dx}{|\Omega|}$

Then $\dfrac{\int_\Omega m\phi\, dx}{\int_\Omega \phi\, dx} = \dfrac{\overline{m\phi}}{\bar{\phi}} = \bar{m} + \dfrac{\text{Cov}(m,\phi)}{\bar{\phi}} \quad \left(\begin{array}{l}\text{"scale transition"}\\ \text{Chesson}\end{array}\right)$

Population Interactions (scale T)

Suppose that u and v are competing populations that on a single time scale would be described by

$$\frac{\partial u}{\partial t} = L_1 u + [a(x) - b(x)u - c(x)v]u$$

$$\frac{\partial v}{\partial t} = L_2 v + [d(x) - e(x)u - f(x)v]v.$$

Using the **rescaled** system where $u = U(t)\phi_1(x)$, $v = V(t)\phi_2(x)$

with ϕ_i the **normalized** eigenfunction of $L_i = 0$, $i = 1,2$
and U = total population for u, V = total population for v

gives

$$\frac{dU}{dT} = \left[\left(\int_\Omega a\phi_1\right) - \left(\int_\Omega b\phi_1^2\right)U - \left(\int_C c\phi_1\phi_2\right)V\right]U$$

$$\frac{dV}{dT} = \left[\left(\int_\Omega d\phi_2\right) - \left(\int_\Omega e\phi_1\phi_2\right)U - \left(\int_\Omega f\phi_2^2\right)V\right]V.$$

This allows comparison of dispersal strategies if the species have similar ecology, so that $a = d$, $b = c = e = f$

Evolution (long timescale)

Approach (motivated by adaptive dynamics)

- Evolution occurs as an initially small population of mutants with better adaptation invades and replaces a resident population
- This occurs rarely relative to the timescale T of ecological interactions
- The traits that will evolve are those that allow a population using them to resist invasion by populations with other traits (Evolutionarily steady strategies or ESS)

Evolution (pairwise invasion analysis)

(Assume resident and invader differ only in their dispersal pattern)

For
$$\frac{dU}{dT} = \left[\left(\int_\Omega \phi_1 m \right) - \left(\int_\Omega \phi_1^2 \right) U - \left(\int_\Omega \phi_1 \phi_2 \right) V \right] U \qquad \left(\int_\Omega \phi_j \, dx = 1 \right)$$

$$\frac{dV}{dT} = \left[\left(\int_\Omega \phi_2 m \right) - \left(\int_\Omega \phi_1 \phi_2 \right) U - \left(\int_\Omega \phi_2^2 \right) V \right] V$$

the semitrivial equilibrium $(U^*, 0)$ has $U^* = \int_\Omega \phi_1 m / \int_\Omega \phi_1^2$

(as $T \to \infty$)

so the competing population V can invade $(U^*, 0)$ if

$$\sigma = \left(\int_\Omega \phi_2 m \right) - \left[\left(\int_\Omega \phi_1 \phi_2 \right) \left(\int_\Omega \phi_1 m \right) / \int_\Omega \phi_1^2 \right] > 0.$$

Observation: This approach cannot distinguish between strategies that produce the same distributions (ϕ_i's), for example L and DL for constant D. It can distinguish diffusion from diffusion + advection

Evolution (continued)

An evolutionarily steady class of strategies

Suppose that $m(x) > 0$, and $\phi_1(x) = \dfrac{m(x)}{\bar{m}}$ $\left(\begin{array}{l}\text{motivated by the}\\ \text{ideal free distribution}\end{array}\right)$

(This will be true for $L_1 = \nabla \cdot \mu(x) \nabla(u/m)$, which includes

$L_1 = \nabla \cdot [\nabla u - u \dfrac{\nabla m}{m}]$ for $\mu = m$ or $L_1 = \Delta(u/m)$ for $\mu = 1$)

The criterion for stability of $(U^*, 0)$ gives

$$\dfrac{\displaystyle\int_\Omega \phi_2 \, m - \left(\displaystyle\int_\Omega \dfrac{m}{\bar{m}} \phi_2\right)\left(\displaystyle\int_\Omega \dfrac{m^2}{\bar{m}}\right)}{\displaystyle\int_\Omega \dfrac{m^2}{\bar{m}^2}} = 0 \qquad \text{(neutral stability)}$$
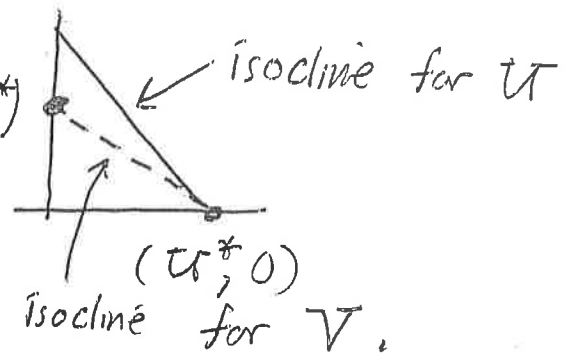
The criterion for stability of $(0, V^*)$ is given by

$$\sigma = \dfrac{1}{\bar{m}}\left[\displaystyle\int_\Omega m^2 - \dfrac{\left(\displaystyle\int_\Omega m\phi_2\right)^2}{\displaystyle\int \phi_2^2}\right] \cdot \text{ By Hölder's inequality,}$$

$\sigma > 0$ if $m^2 \neq k\, m\phi_2$,
that is, $m \neq k\phi_2$, for
some constant k. (unstable!)

Evolution (continued)

It turns out that if $\phi_1 = \dfrac{m(x)}{\overline{m}}$, solving for a possible positive equilibrium in the fast dispersal system gives $V = 0$.

Phase portrait: $(0, V^*)$

isocline for U

isocline for V.

$(U^*, 0)$

It follows that U excludes V.

Thus, since ϕ_2 is arbitrary, strategies that yield $\phi_1 = \dfrac{m(x)}{\overline{m}}$ are evolutionarily steady relative to those that do not. *

(* Related results for patch models, nonlocal models, reaction-diffusion-advection exist but take <u>much</u> more math.)

References

Case 1: R.S. Cantrell and C., SIAM Review 38 (1996), 256-286.

Case 2: R.S. Cantrell, C., M. Lewis, Y. Lou, JMB, epub,
DOI: 10.1007/s00285-18-1302-02