Transients and time scales in the dynamics and management of ecological systems

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Caricature of much of 'classical' ecological theory (Lotka, Volterra …)

Simple model that is deterministic and has no explicit dependence of parameters on time

$$\frac{dx}{dt} = f(x,y)$$
$$\frac{dy}{dt} = g(x,y)$$

Stable equilibrium (asymptotic behavior)

"Natural" ecological system

Caricature of much of ‘classical’ ecological theory

Simple model that is deterministic and has no explicit dependence of parameters on time

$$\frac{dx}{dt} = f(x, y)$$
$$\frac{dy}{dt} = g(x, y)$$

Stable equilibrium

“Natural” ecological system

So, key issues

- Transient dynamics
- Non-autonomous systems
- (Realistic) approaches to stochasticity

Transient dynamics of ecological systems key for management

- Time scales of social systems
- Time scales of ecological systems – hard to change
- Time scales for decision makers

First, a bit of (neglected) history

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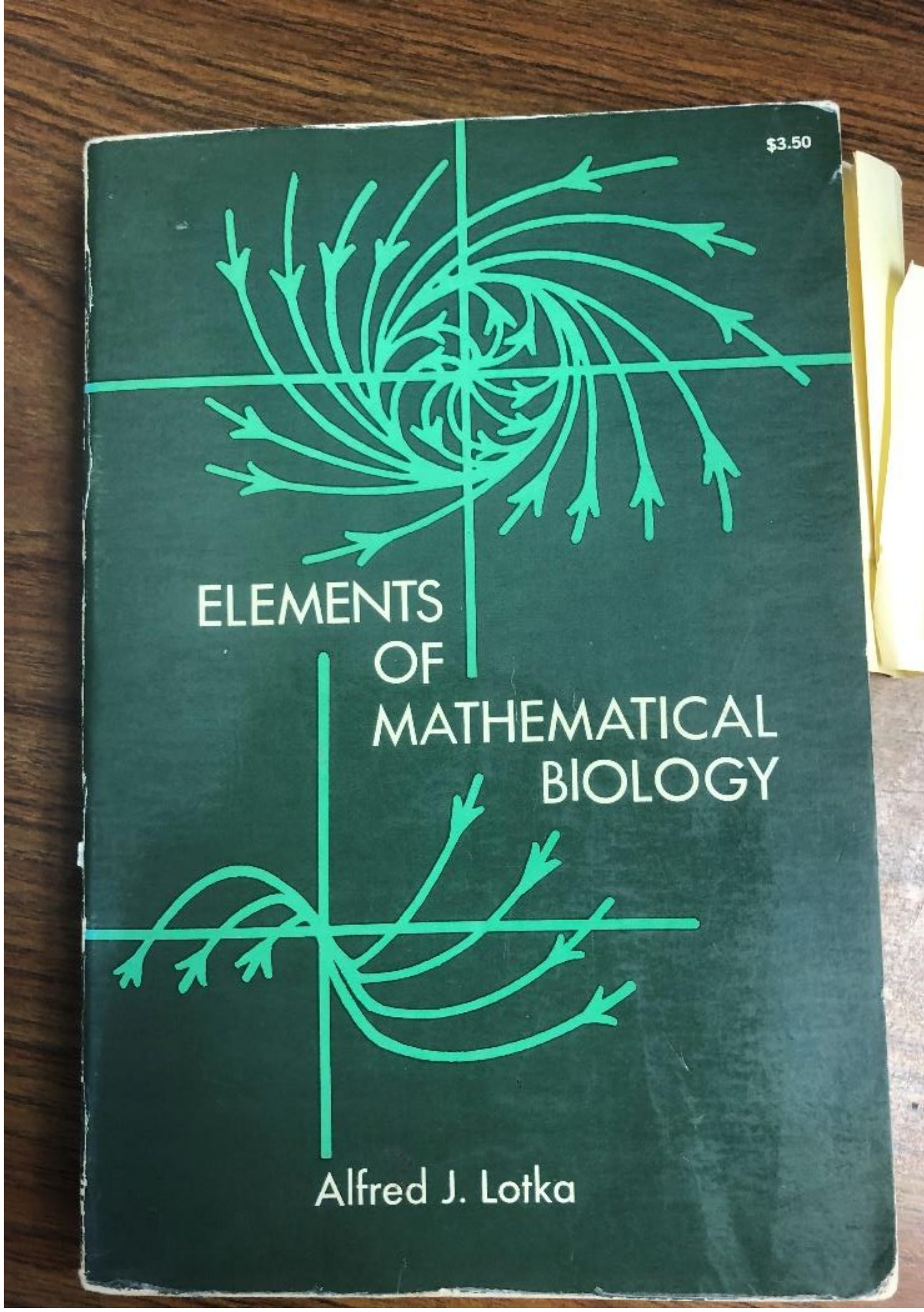

a function of both N_1 and N_2, the ... the
number of the parasite population.

The birth of a parasite is contingent upon the laying of an egg in a host, and the ultimate killing of the host thereby. To simplify matters we will consider the case in which only one egg is hatched from any invaded host. If an egg is hatched from every host killed by the invasion, then the total birthrate in the parasite population is evidently kN_1N_2. If only a fraction k' of the eggs hatch, then the total birthrate in the parasite population is evidently $kk' N_1N_2$, which we will denote briefly by KN_1N_2. Lastly, let the deathrate per head among the parasites be d_2. Then we have, evidently

$$\left.\begin{aligned} \frac{dN_1}{dt} &= r_1N_1 - kN_1N_2 \\ \frac{dN_2}{dt} &= KN_1N_2 - d_2N_2 \end{aligned}\right\} \tag{27}$$

where r_1 has been written for $(b_1 - d_1)$.

Regarding the function k, we shall now make the very broad assumption that it can be expanded as power series in N_1 and N_2, thus

$$k = \alpha + \beta N_1 + \gamma N_2 + \ldots \tag{28}$$

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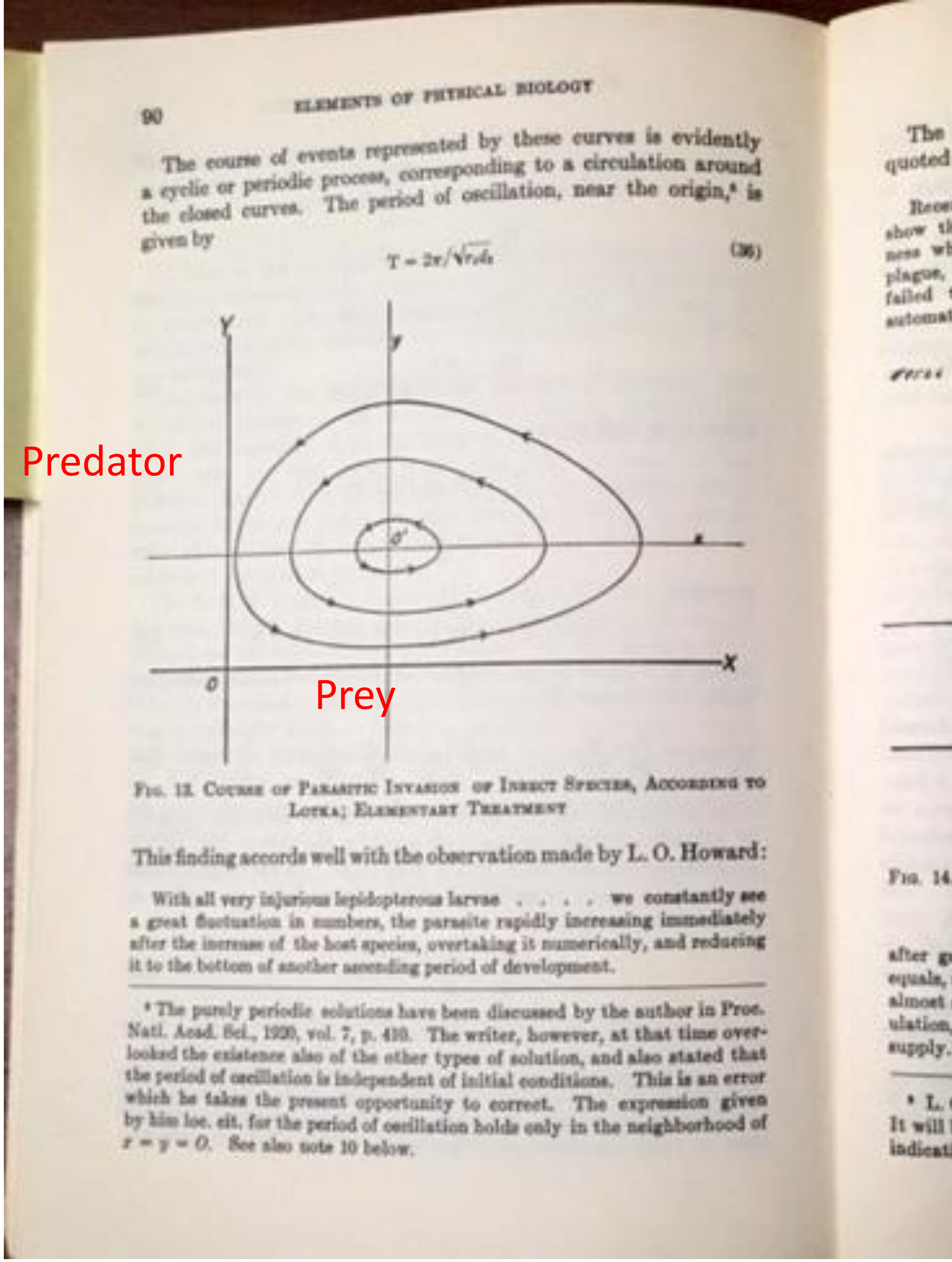
$$k = \alpha + \beta N_1 + \gamma N_2 + \dots \qquad (28)$$

Lotka-Volterra – simple oscillations



90 ELEMENTS OF PHYSICAL BIOLOGY

The course of events represented by these curves is evidently a cyclic or periodic process, corresponding to a circulation around the closed curves. The period of oscillation, near the origin,[8] is given by

$$T = 2\pi/\sqrt{r_1 d_2} \qquad (36)$$

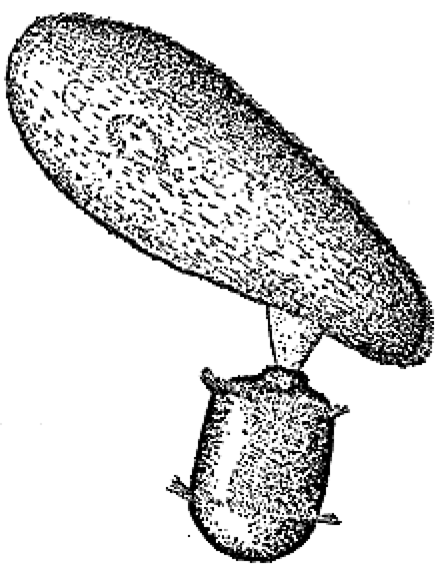
FIG. 13. COURSE OF PARASITIC INVASION OF INSECT SPECIES, ACCORDING TO LOTKA; ELEMENTARY TREATMENT

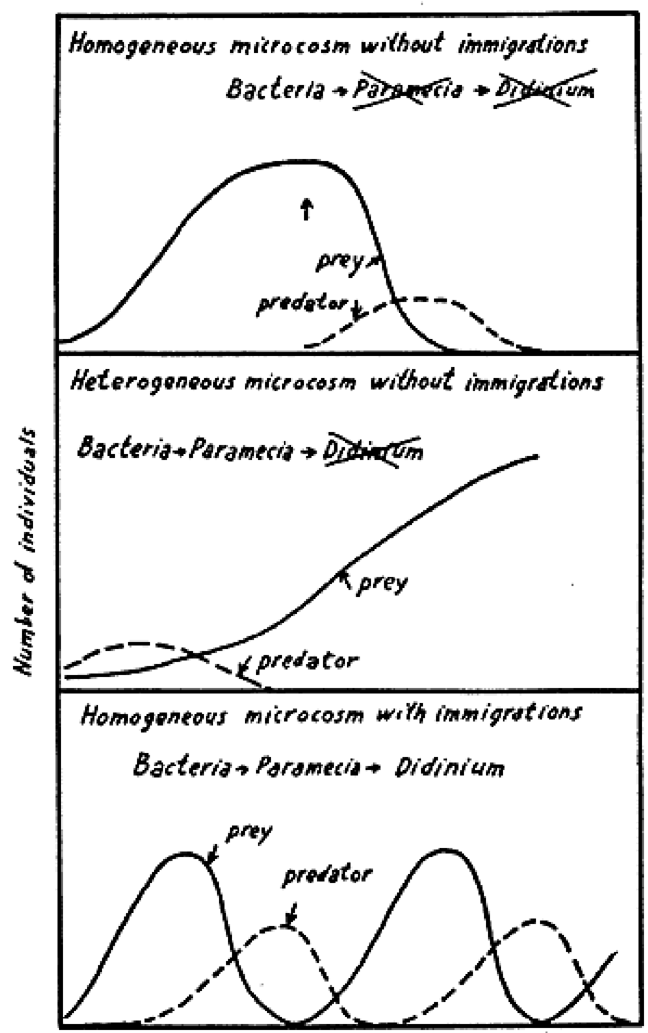
This finding accords well with the observation made by L. O. Howard:

With all very injurious lepidopterous larvae . . . . . we constantly see a great fluctuation in numbers, the parasite rapidly increasing immediately after the increase of the host species, overtaking it numerically, and reducing it to the bottom of another ascending period of development.

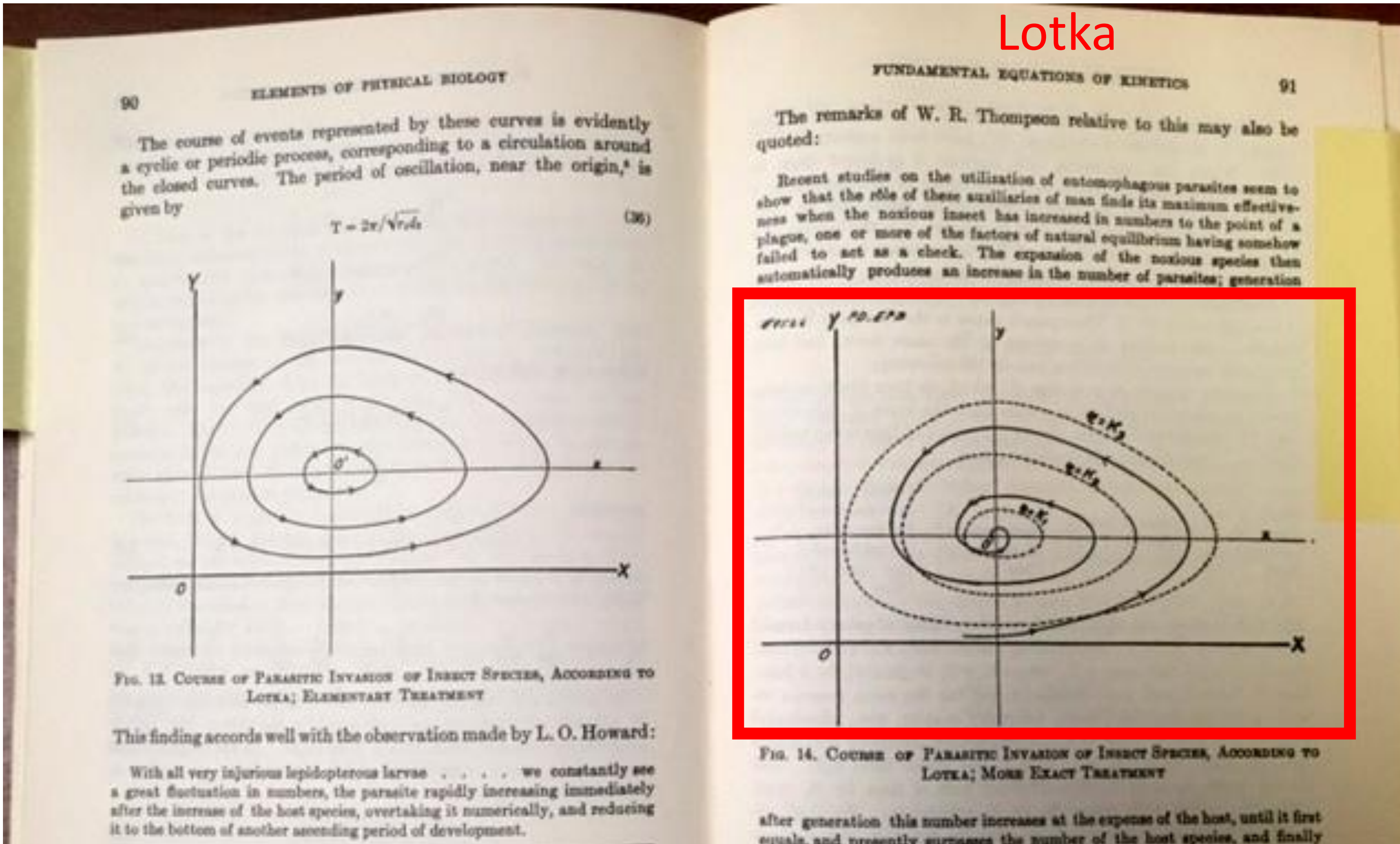
[8] The purely periodic solutions have been discussed by the author in Proc. Natl. Acad. Sci., 1920, vol. 7, p. 410. The writer, however, at that time overlooked the existence also of the other types of solution, and also stated that the period of oscillation is independent of initial conditions. This is an error which he takes the present opportunity to correct. The expression given by him loc. cit. for the period of oscillation holds only in the neighborhood of $x = y = O$. See also note 10 below.

Even simple lab systems are different (but see Blasius et al, Nature 2019)





Time scales –longer time scale on right-so oscillations are a transient



Epidemiology

A Contribution to the Mathematical Theory of Epidemics.

By W. O. Kermack and A. G. McKendrick.

(Communicated by Sir Gilbert Walker, F.R.S.—Received May 13, 1927.)

(From the Laboratory of the Royal College of Physicians, Edinburgh.)

Introduction.

A Contribution to the Mathematical Theory of Epidemics.

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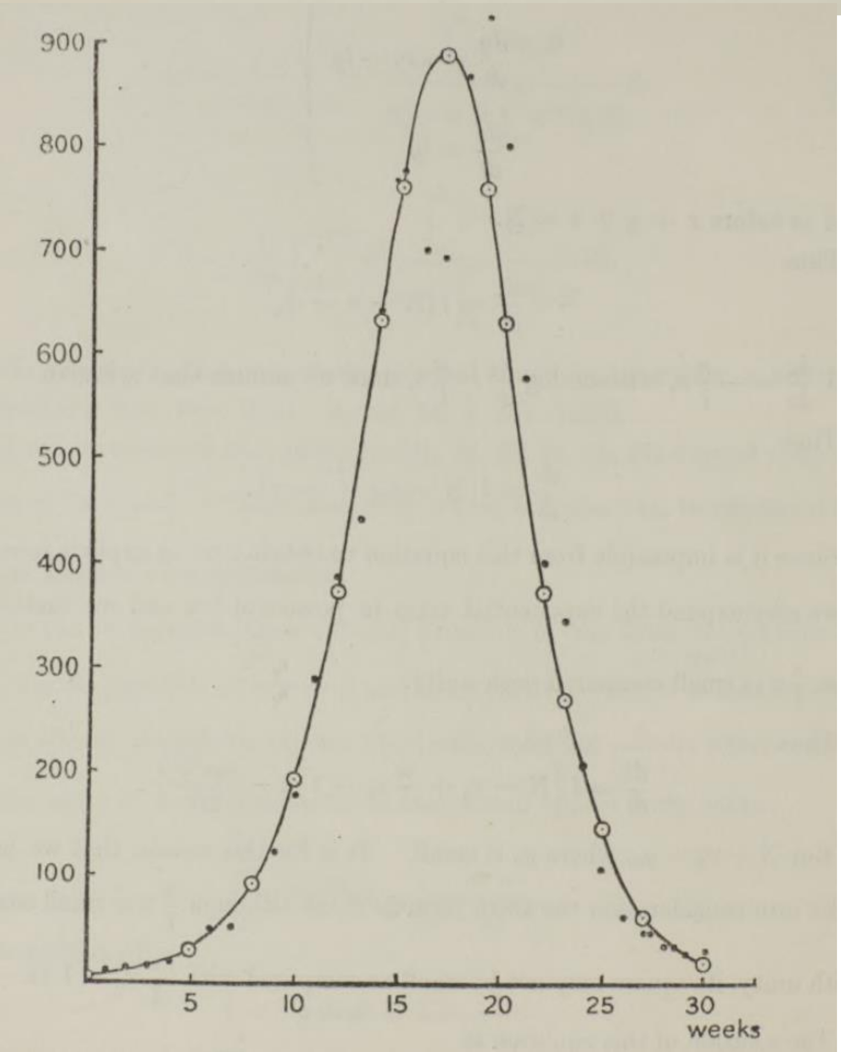

Solid line is model output from a simple SIR model.
Solid small dots are data – death from plague in Mumbai (then in English called Bombay).
Model assumes that population size is constant, so assumes separation of time scales.

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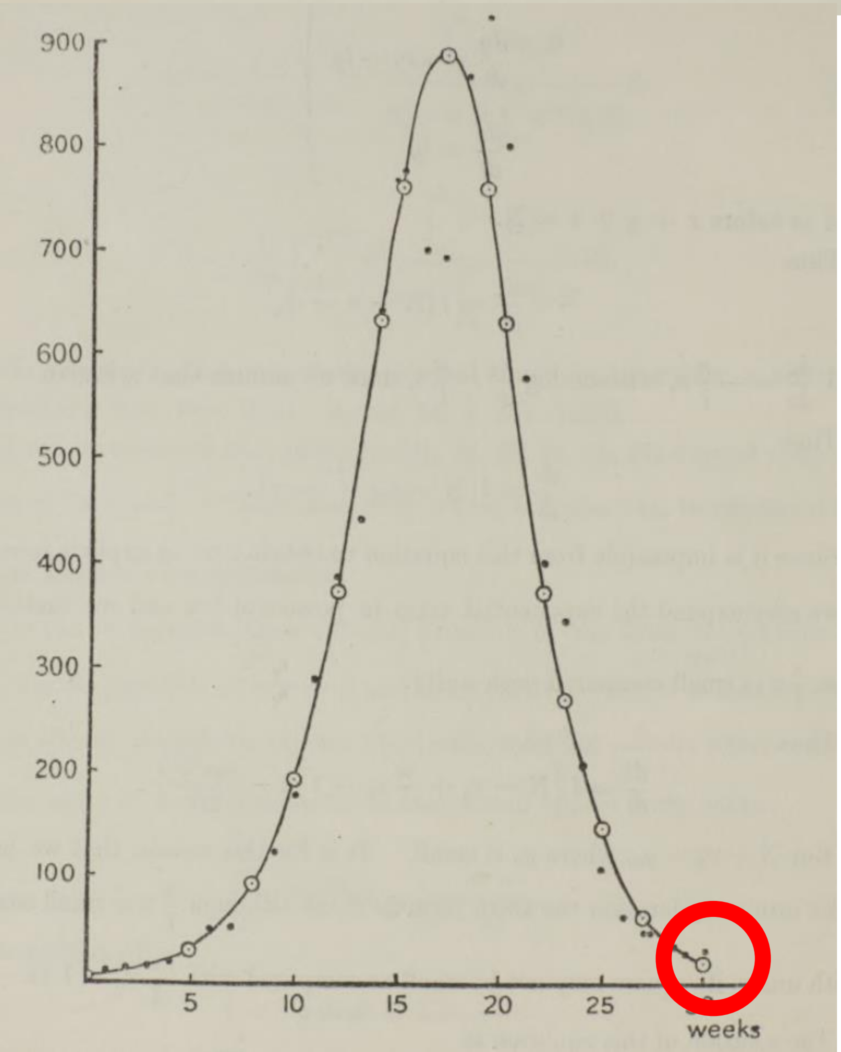

The asymptotic behavior is less important since it is simply that there are no deaths at the end of the epidemic

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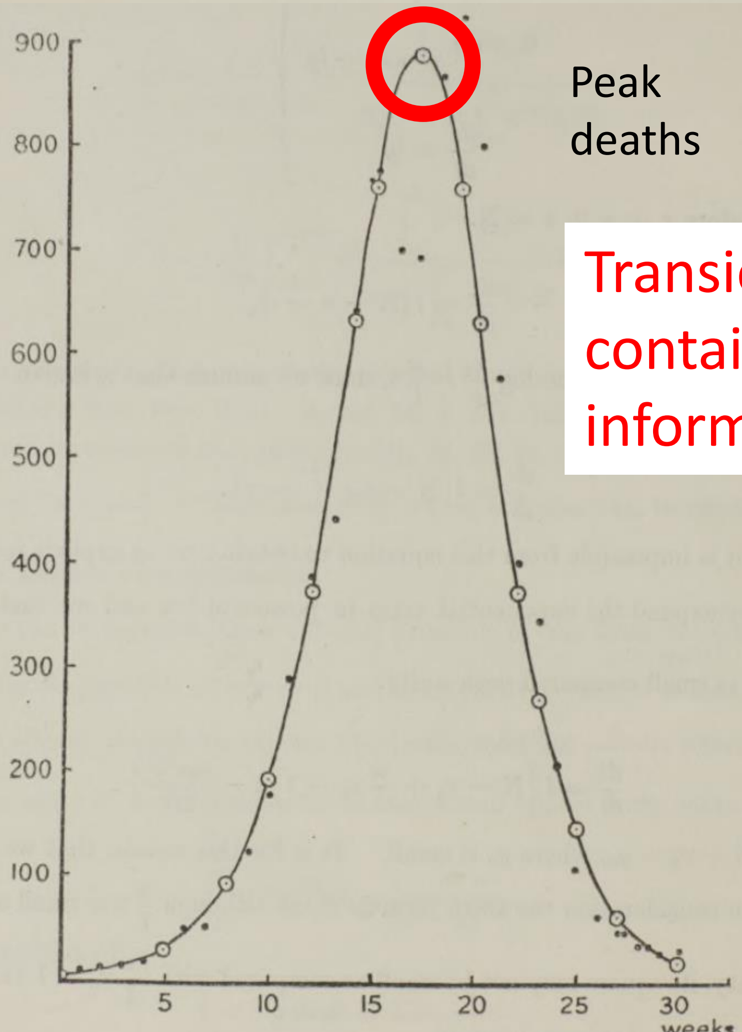
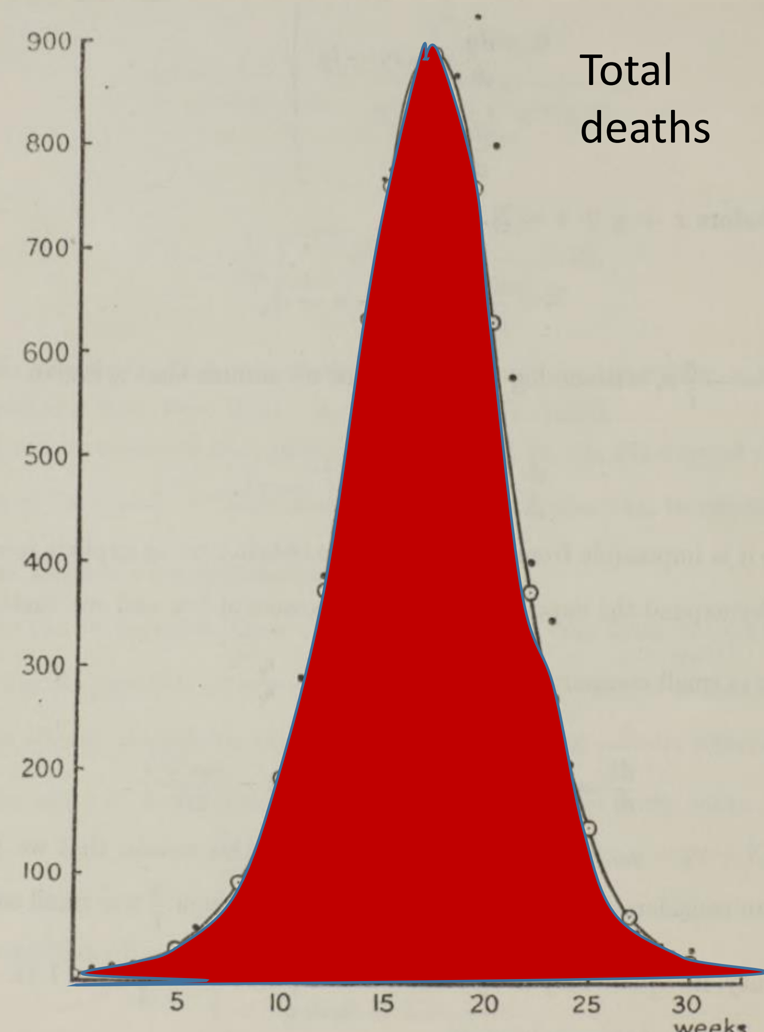


Peak deaths

Transients contain the key information



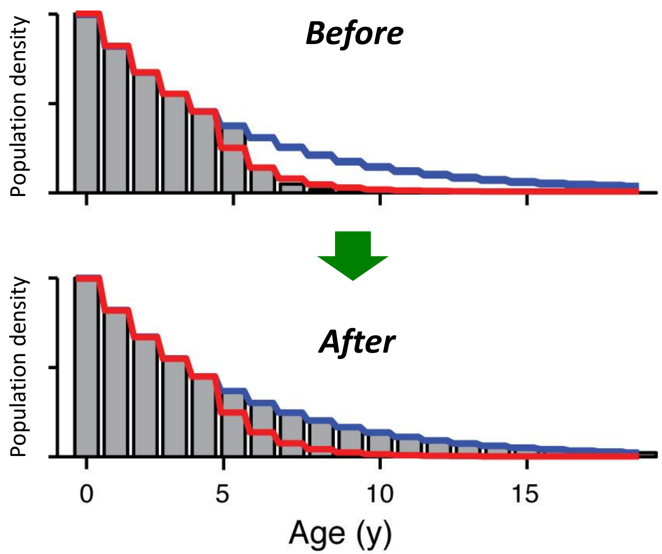
Total deaths

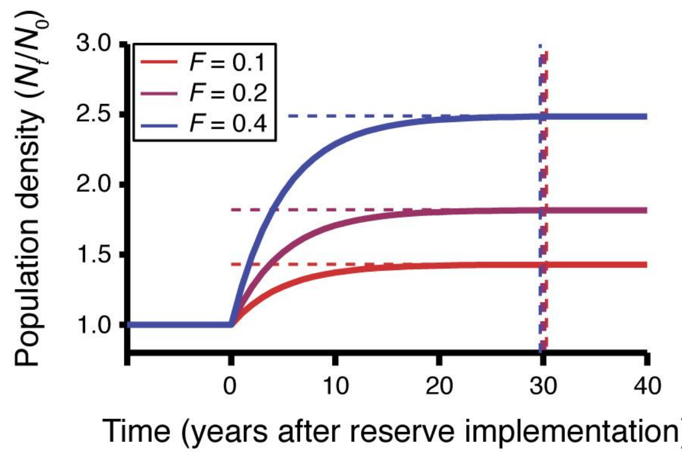
‘Linear transients’ are important for marine protected areas

Adaptive management of MPAs: Theory

Models can show how abundance will change: How much and when

‘Filling in’ the age distribution is the <u>first response</u> to MPAs





Max increase: $$\lim_{t \to \infty} \frac{N_t}{N_0} = \frac{M + F}{M}$$

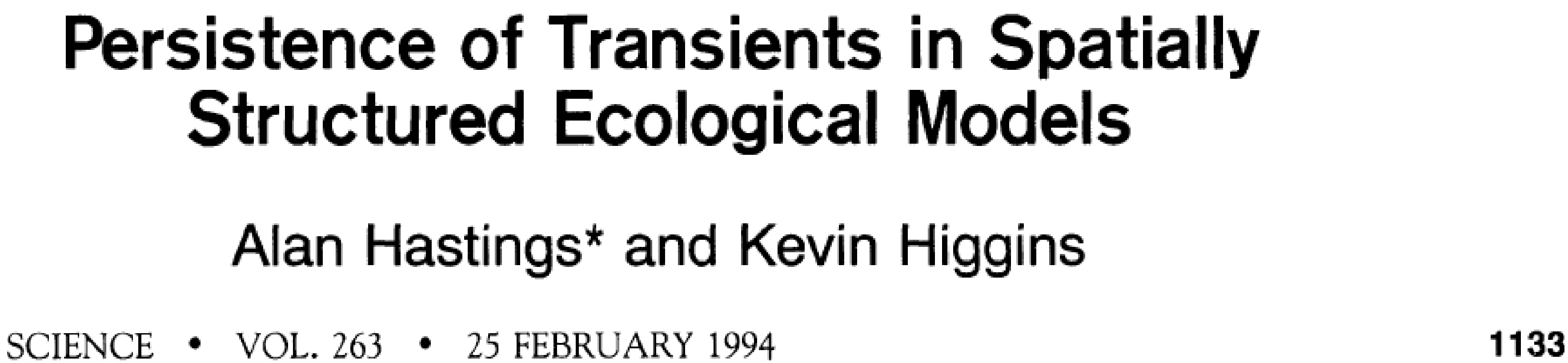
M = natural mortality rate;

F = fishing harvest rate

Time scale of filling in: e^{-M}

White et al. (2013) *Conservation Letters*

So even ‘density independent’ transients are important, but of course more complex with density dependence


Persistence of Transients in Spatially Structured Ecological Models

Alan Hastings* and Kevin Higgins

SCIENCE • VOL. 263 • 25 FEBRUARY 1994 1133

Movement of larvae by dispersal, finite habitat

$$N(t+1,x) = \int_0^L l(t,y)g(y,x)dy$$

Local production of larvae

$$l(t, y) = N(t,y) \exp (r(1-N(t,y)))$$

Dispersal kernel

$$g(y,x) = \frac{\exp(-D(y-x)^2)}{\sqrt{\pi/D}}$$

$D = 800$

"Simple" model with very long transients – high dimension due to space

Plot of overall numbers vs time shows long transients

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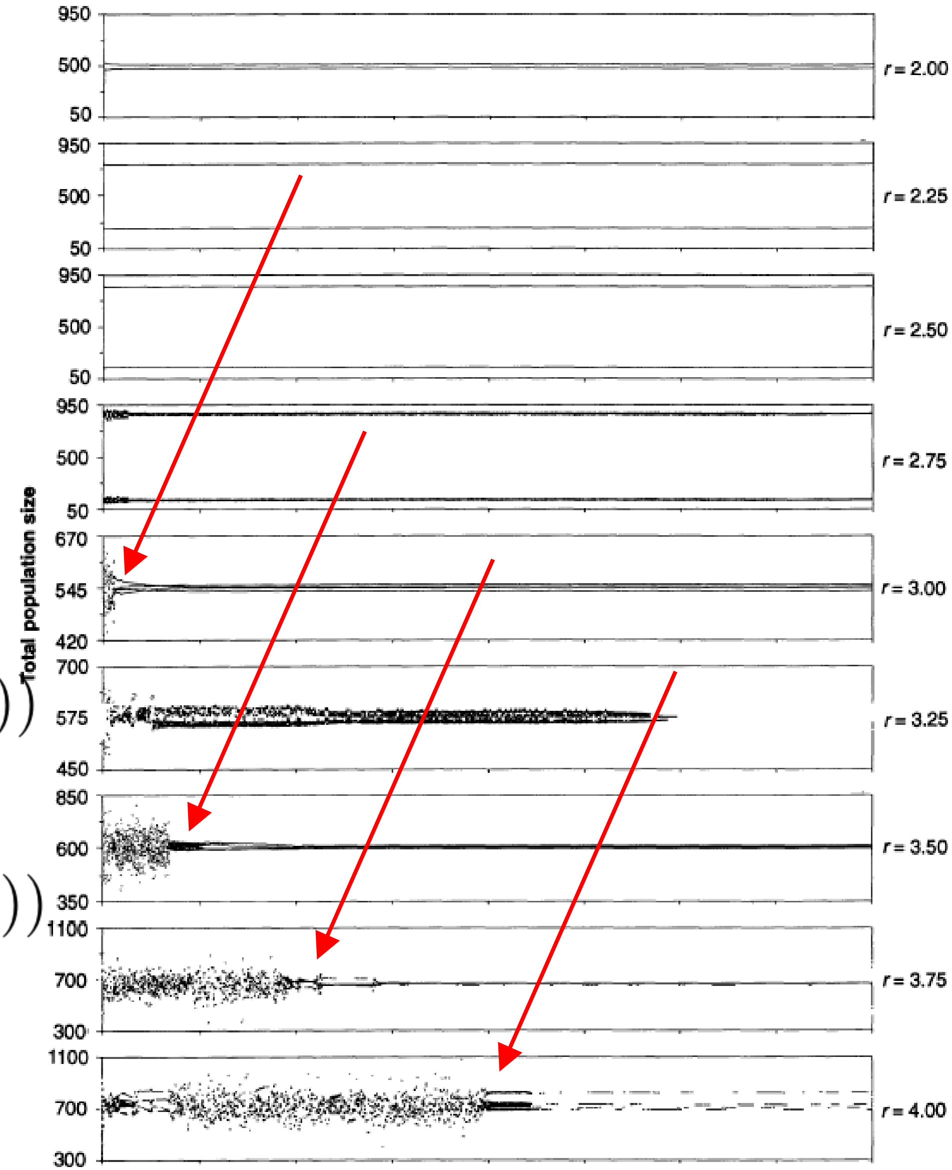


0 20,000

Time

plots for increasing values of r down the slide

Time scale over which two weakly coupled oscillators (predator prey systems with low dispersal rates) synchronize can be long

$$\frac{\mathrm{d}H_i}{\mathrm{d}t} = rH_i(1 - H_i/K) - \frac{aP_iH_i}{b+H} + D_{\mathrm{H}}(H_j - H_i)$$

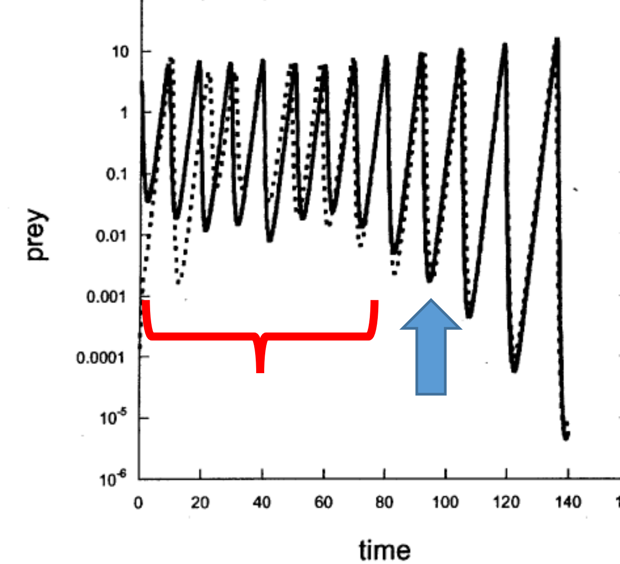
$$\frac{\mathrm{d}P_i}{\mathrm{d}t} = \frac{caP_iH_i}{b+H_i} - mP_i + D_{\mathrm{P}}(P_j - P_i).$$

Ecology Letters, (2001) **4**: 215–220

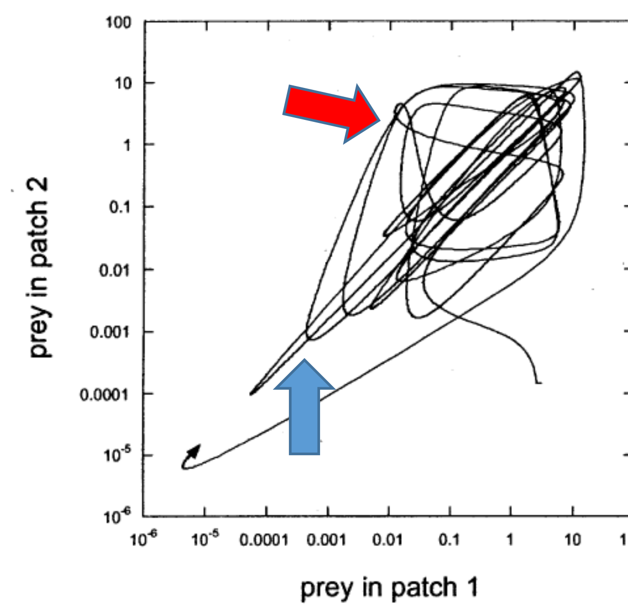
REPORT

Transient dynamics and persistence of ecological system

Alan Hastings

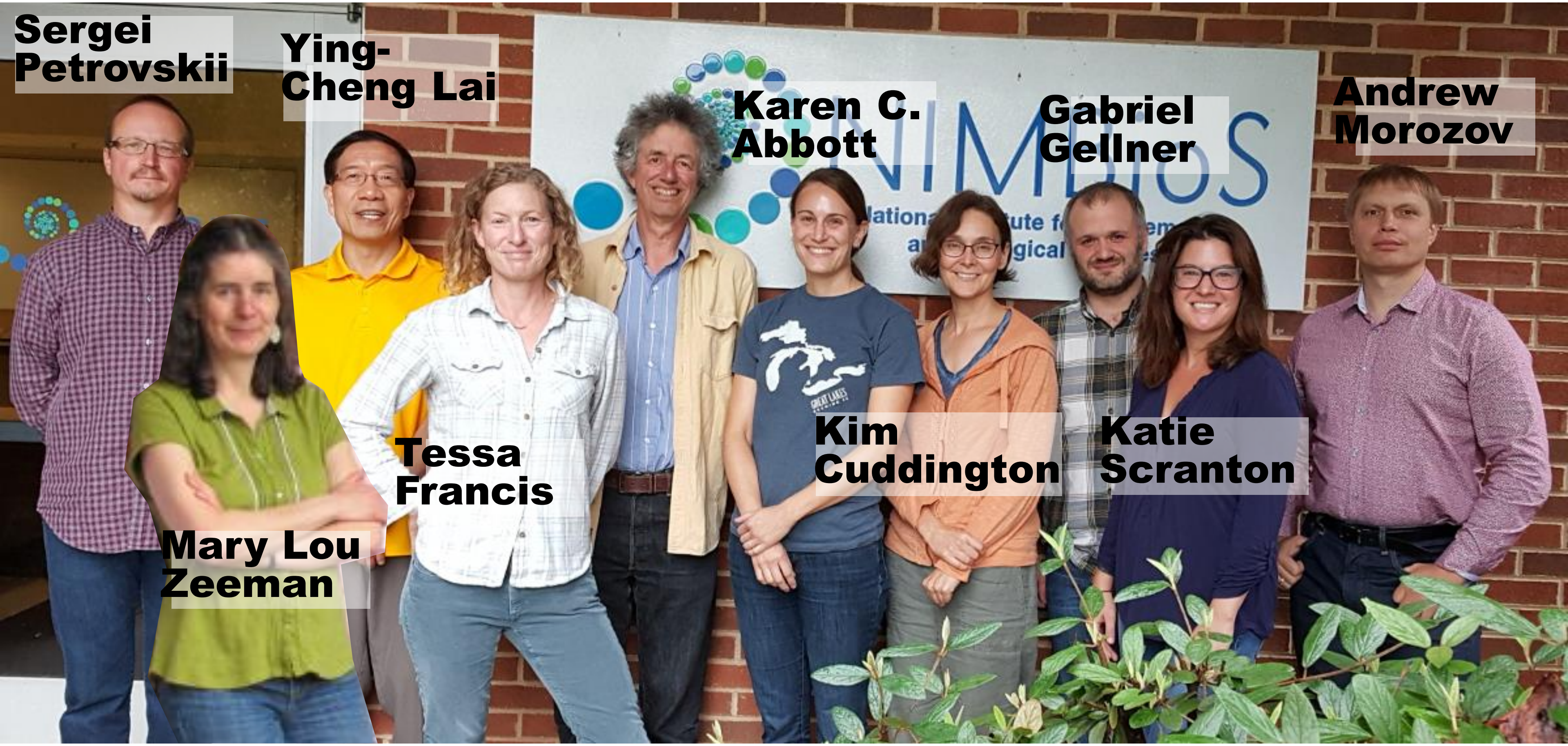


Dashed line is patch one, solid line is patch two



Examples show importance of transients, but can we make studies of transients systematic for nonlinear systems?

- What are the characteristics of ecological systems that we would expect would produce transients?
- Important for understanding experiments and management (often done on relatively short time scales)


Sergei Petrovskii
Ying-Cheng Lai
Karen C. Abbott
Gabriel Gellner
Andrew Morozov
Tessa Francis
Kim Cuddington
Katie Scranton
Mary Lou Zeeman

nature ecology & evolution
PERSPECTIVE
https://doi.org/10.1038/s41559-020-01365-0
Check for updates

Transient phenomena in ecology

Alan Hastings[1*], Karen C. Abbott[2], Kim Cuddington[3], Tessa Francis[4], Gabriel Gellner[5], Ying-Cheng Lai[6], Andrew Morozov[7,8], Sergei Petrovskii[7], Katherine Scranton[9], Mary Lou Zeeman[10]

The importance of transient dynamics in ecological systems and in the models that describe them has become increasingly recognized. However, previous work has typically treated each instance of these dynamics separately. We review both empirical examples and model systems, and outline a classification of transient dynamics based on ideas and concepts from dynamical systems theory. This classification provides ways to understand the likelihood of transients for particular systems, and to guide investigations to determine the timing of sudden switches in dynamics and other characteristics of transients. Implications for both management and underlying ecological theories emerge.

Hastings *et al.*, *Science* **361**, eaat6412 (2018)   7 September 2018

Management implications of long transients in ecological systems

Tessa B. Francis[1], Karen C. Abbott[2], Kim Cuddington[3], Gabriel Gellner[4], Alan Hastings[5,6], Ying-Cheng Lai[7], Andrew Morozov[8,9], Sergei Petrovskii[8] and Mary Lou Zeeman[10]

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Review

Long transients in ecology: Theory and applications

Andrew Morozov[a,j], Karen Abbott[b], Kim Cuddington[c], Tessa Francis[d], Gabriel Gellner[e], Alan Hastings[f,k], Ying-Cheng Lai[g], Sergei Petrovskii[a,l,*], Katherine Scranton[h], Mary Lou Zeeman[i]

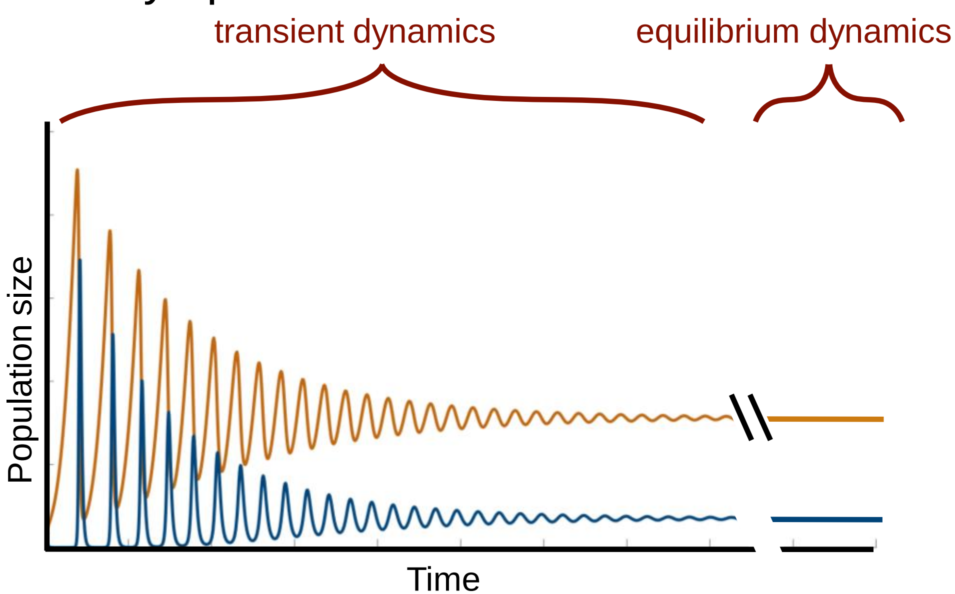
[a] Mathematics, University of Leicester, UK
[b] Biology, Case Western Reserve University, USA

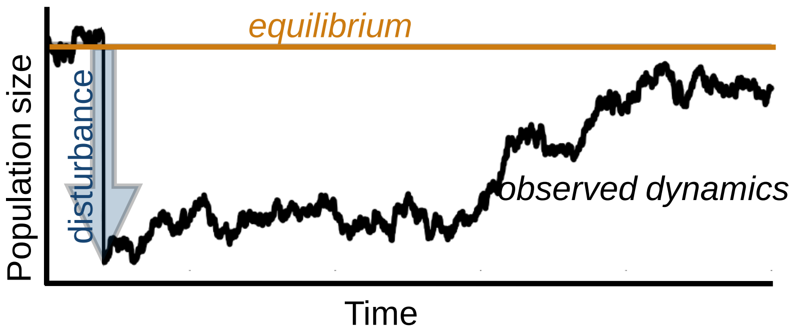
Use ideas from dynamical systems to classify long transients

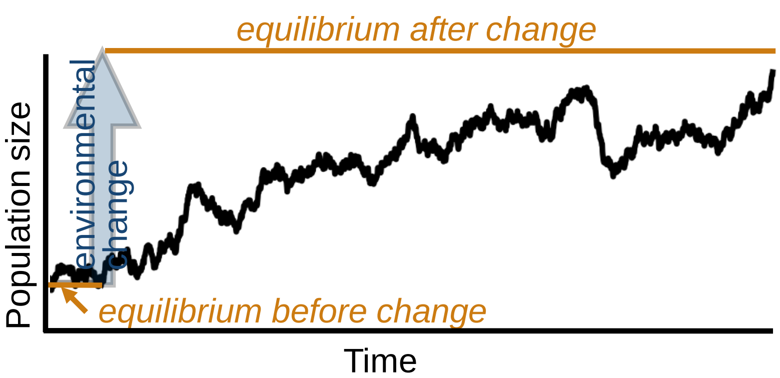
- Show when they will arise

What do we mean by “long transients”?

- Transient: dynamics that occur when a system is not at equilibrium
  - **Equilibrium**: an asymptotic state (point, limit cycle, chaos); a system at this state will stay there indefinitely unless perturbed
- Long transient: a transient that lasts “longer than you’d think”
  - roughly, dozens of generations or more
  - long enough that it really looks like asymptotic behavior







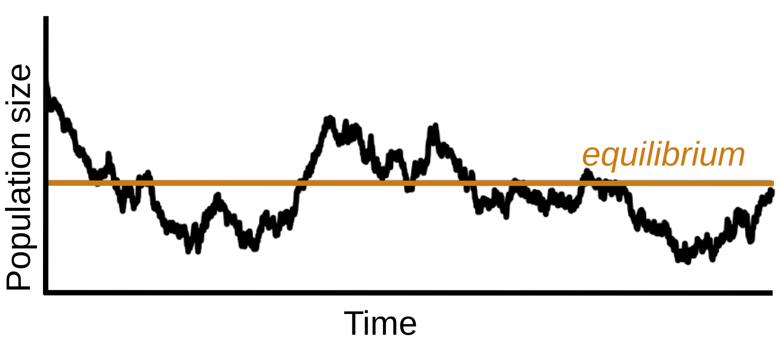
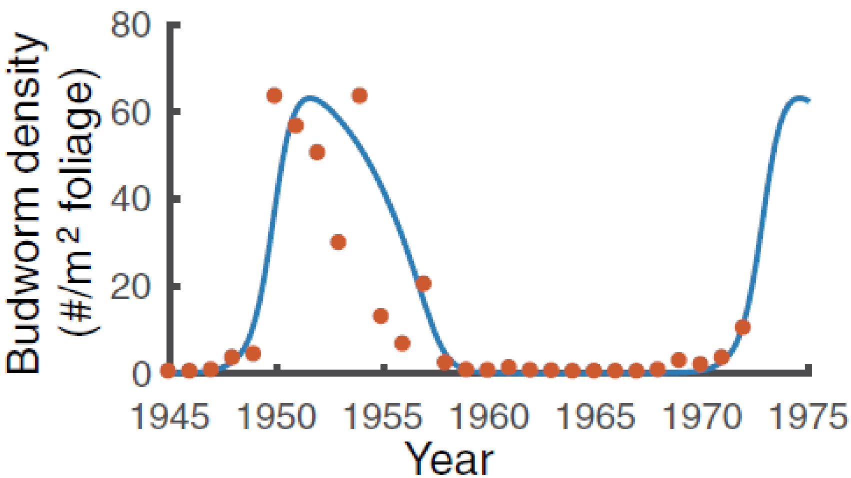


Table 2. Empirical evidence for long ecological transients.

Population(s)	Observed pattern	Duration	
		Generations	Years
Laboratory population of beetles (*Tribolium* spp.) (25)	Switch from a regime with an almost constant density to large-amplitude oscillations	15	~1.5 (70 weeks)
Growth of macrophytes in shallow eutrophic lakes in the Netherlands (46)	Switch from a macrophyte-dominated state to a turbid water state	1 to 5	1 to 5
Population of large-bodied benthic fishes on the Scotian Shelf of Canada's east coast (27)	Switch from a forage fish (and macroinvertebrate)–dominated state to a benthic fish–dominated state	5 to 8	20
Coral and microalgae in the Caribbean (47, 48)	Shifts from coral to macroalgal dominance on coral reefs	20 to 25 (corals); 50 to 100 (macroalgae)	10
Voles, grouse in Europe (59)	Switch between cyclic and noncyclic regimes, or between cyclic regimes with different periodicity	60 (voles); 20 to 30 (lemmings); 5 (grouse)	~30
Dungeness crab (*Cancer magister*) (53)	Large-amplitude transient oscillations with further relaxation to equilibrium	10 to 15	45
Zooplankton-algal interactions in temperate lakes in Germany (26)	Variation of amplitude and period of predator-prey oscillations across the season	80 to 100 (algae); 5 to 8 (zooplankton)	1
Planktonic species in chemostat and temperate lakes (72)	Long-term variation of species densities, with extinction of some species	40 to 100	~0.05 to 0.15 (3 to 8 weeks)
Laboratory microbial communities (56)	Slow switch between alternative stable states	20 to 40	0.11 to 0.21 (6 to 12 weeks)
Grass community in abandoned agricultural fields in the Netherlands (57)	Long-term existence of a large number of alternative transient states	10	9
Extinction debt phenomena as a consequence of habitat loss [plants, birds, fish, lichens, and others (60)]	Long-term extinction of populations, occurring either steadily or via oscillations	20 to 100 (or more)	1 to 100
Fish and invertebrates in watersheds in western North Carolina, USA (49)	Influence of past habitat structure on present biodiversity patterns after restoration	10 to 20 (fish); 40 (invertebrates)	40
Modeled spruce budworm outbreaks in balsam fir forests (2)	Budworm outbreaks driven by slow changes in condition of fir foliage	5 (refoliation); 50+ (budworm)	50

Empirical examples show that transients in fact are widespread in natural (and experimental) systems



Spruce budworm [dots] has a much faster generation time than its host tree, resulting in extended periods of low budworm density interrupted by outbreaks.

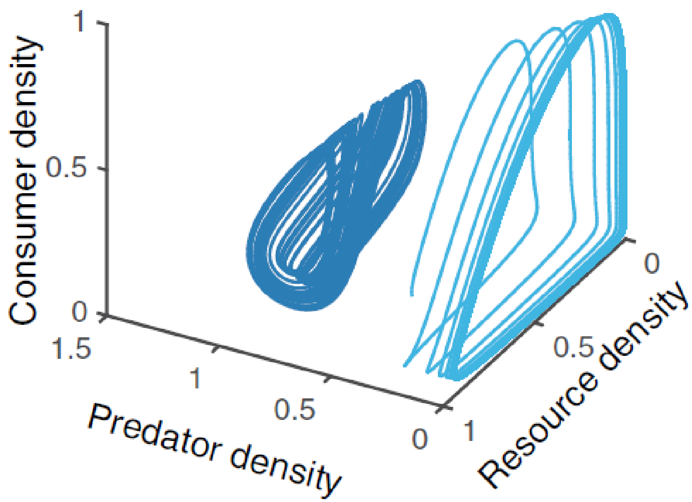
Data from NERC Centre for Population Biology, Imperial College, Global Population Dynamics Database (1999)

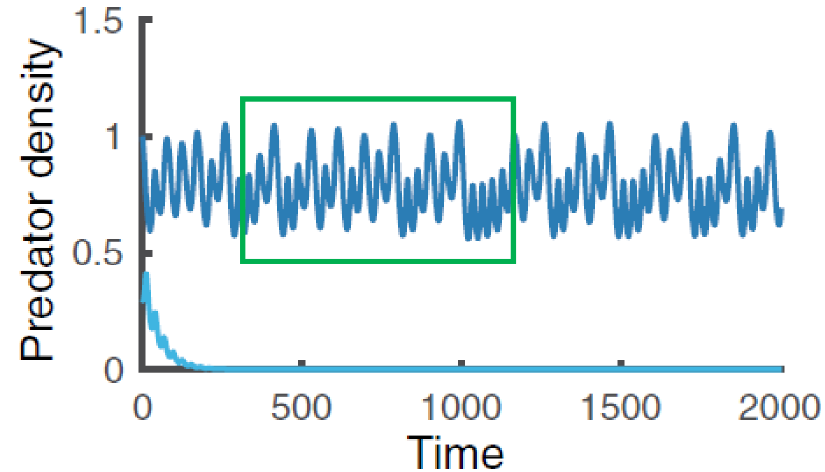
Model [blue] from D. Ludwig, D. D. Jones, C. S. Holling, Qualitative analysisof insect outbreak systems: The spruce budworm and forest. J. Anim. Ecol. 47, 315–332 (1978).

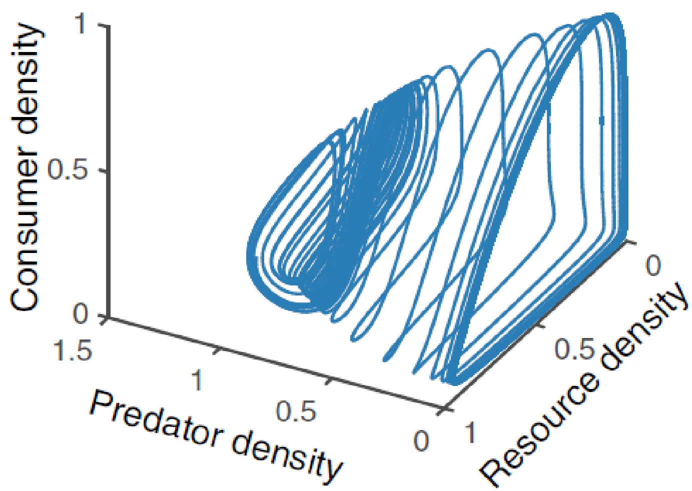
Dynamical systems ideas can help to ‘classify’ transients

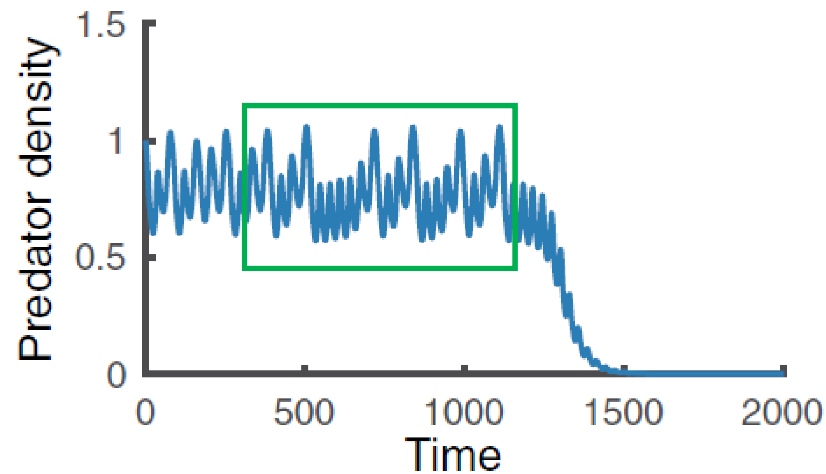
- Ghost attractor

Illustration of ghost attractor in 3 species food chain(3 ODE's)



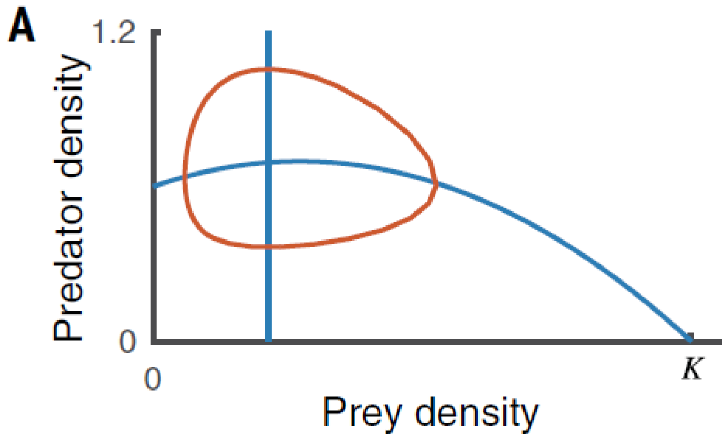




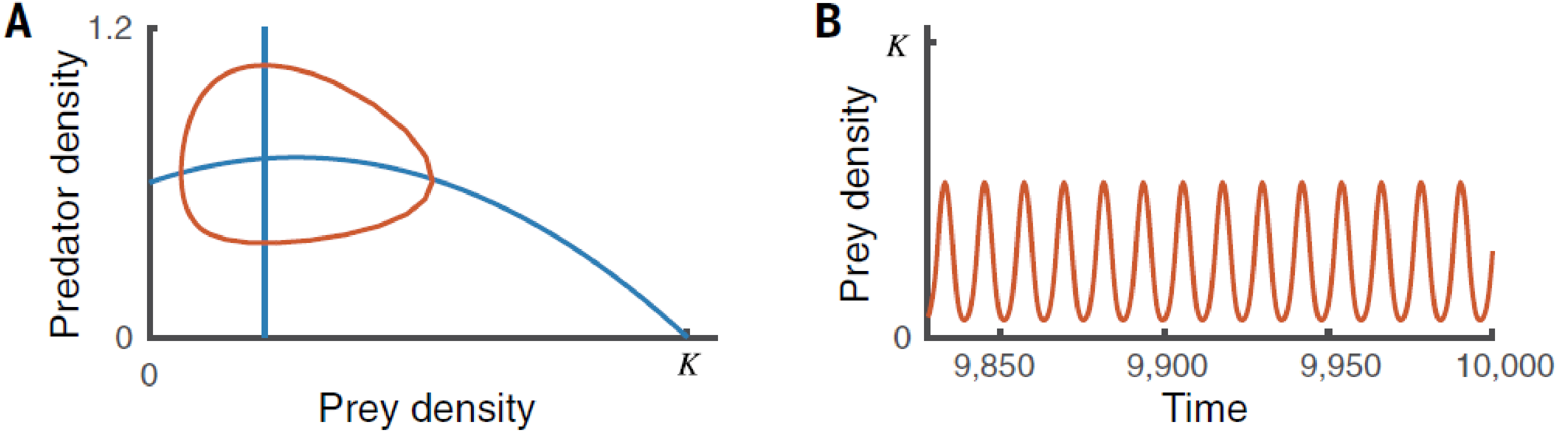


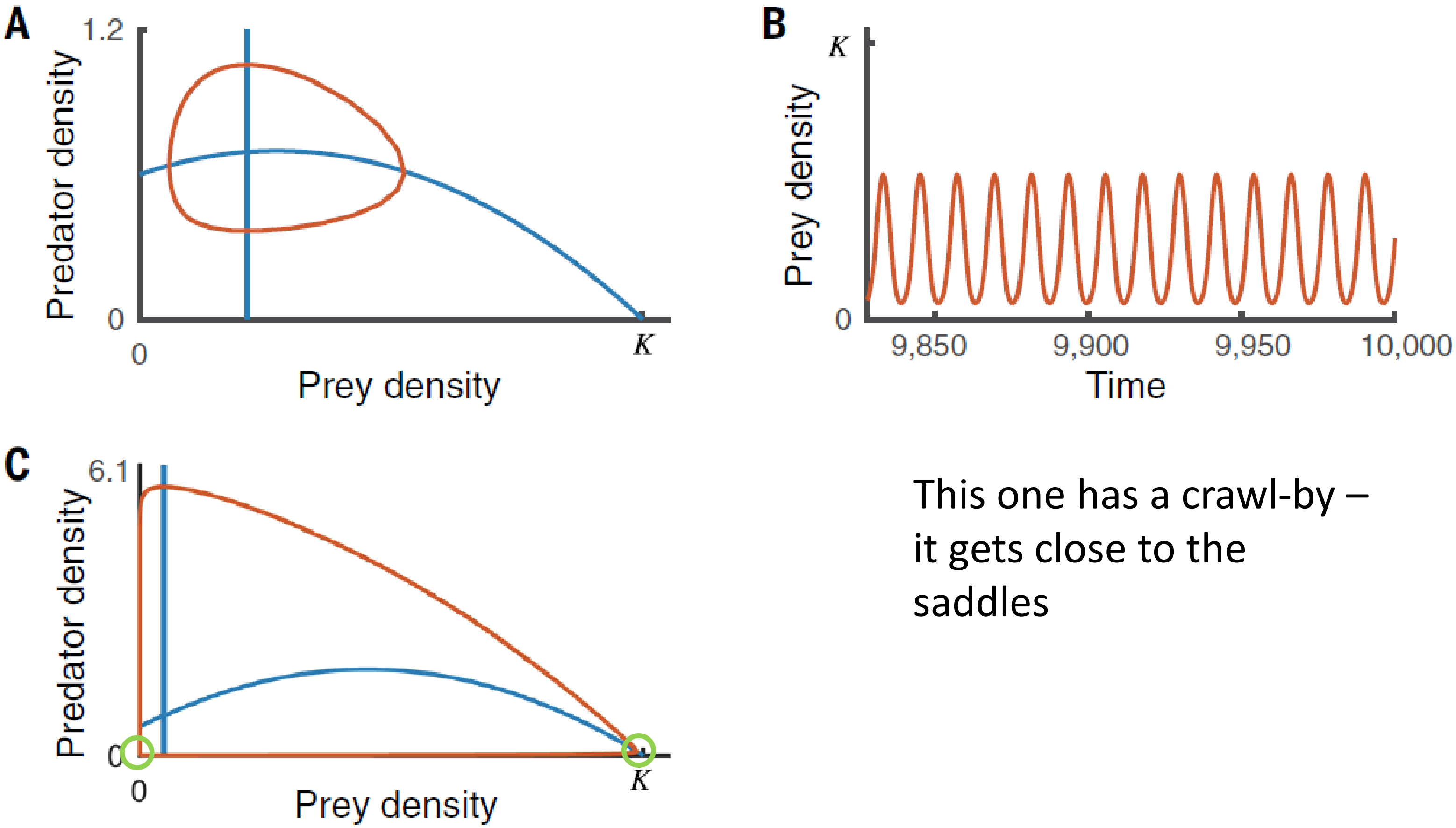
Predator-Prey dynamics

- $dH/dt = rH(1-H) - f(H)P$
- $dP/dt = cf(H) - P$
- Illustrate with phase planes

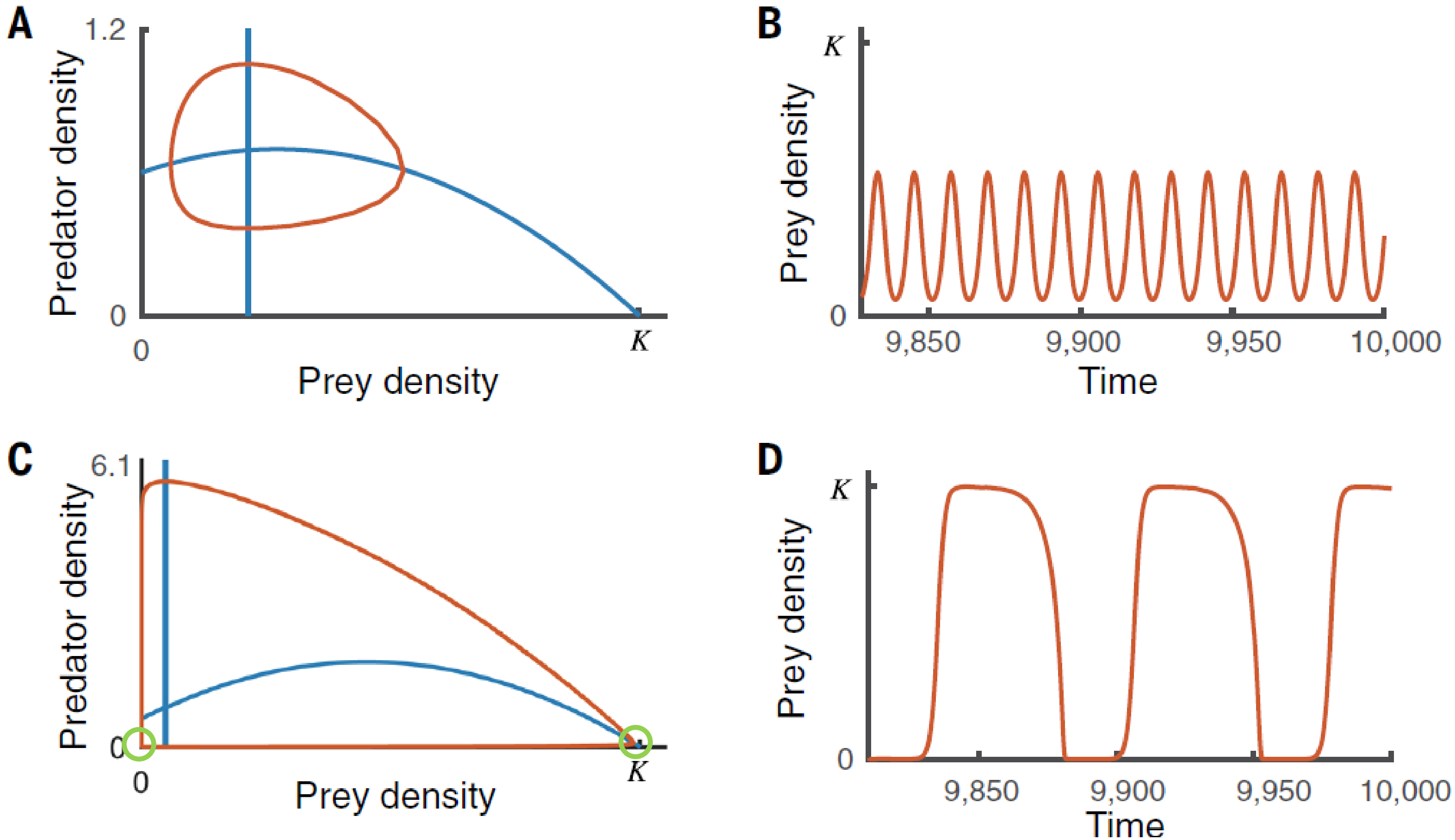


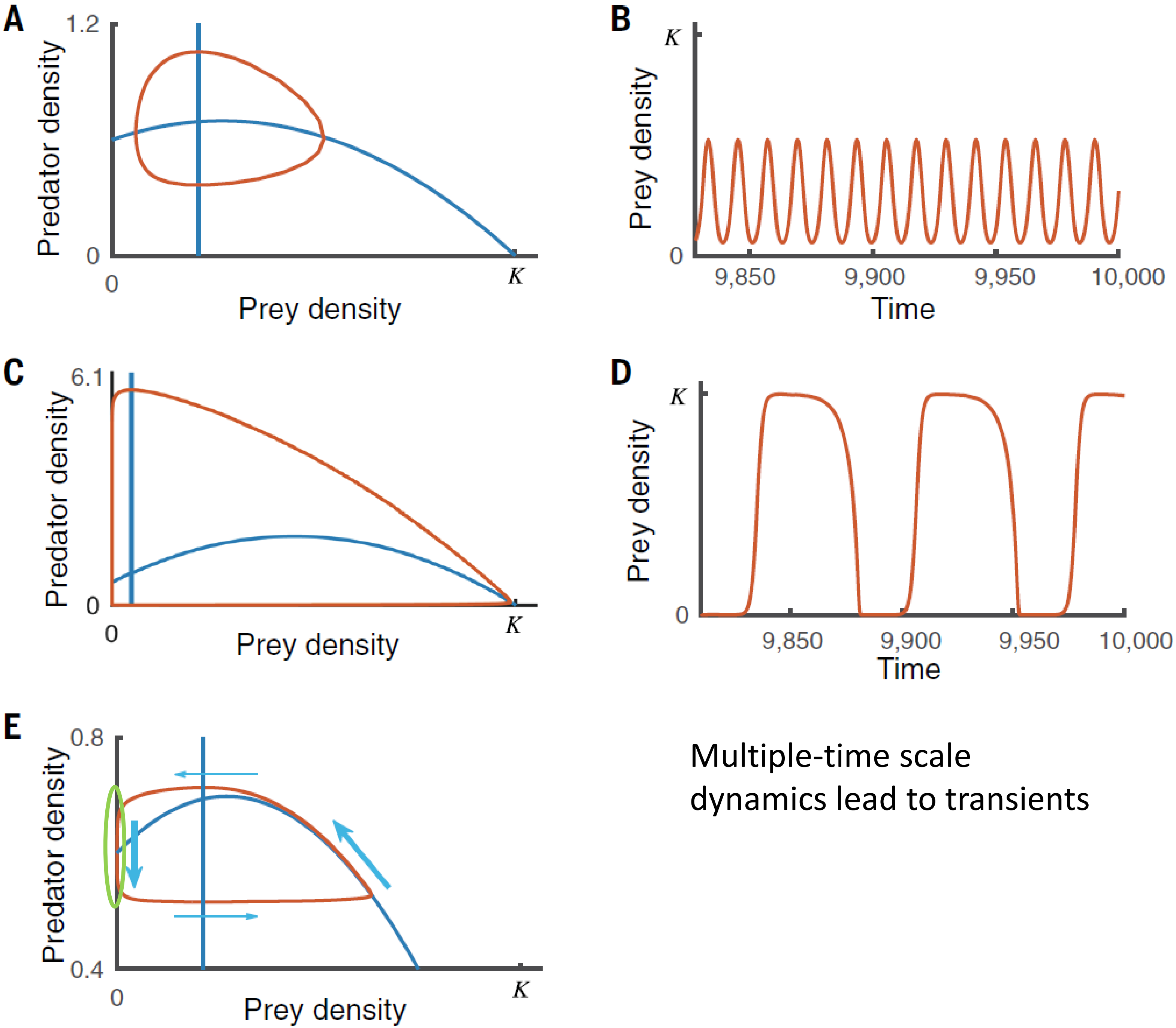
No transients for this predator prey dynamic as illustrated in a phase plane


A
1.2
0
Predator density
0
K
Prey density
B
K
0
Prey density
9,850
9,900
9,950
10,000
Time

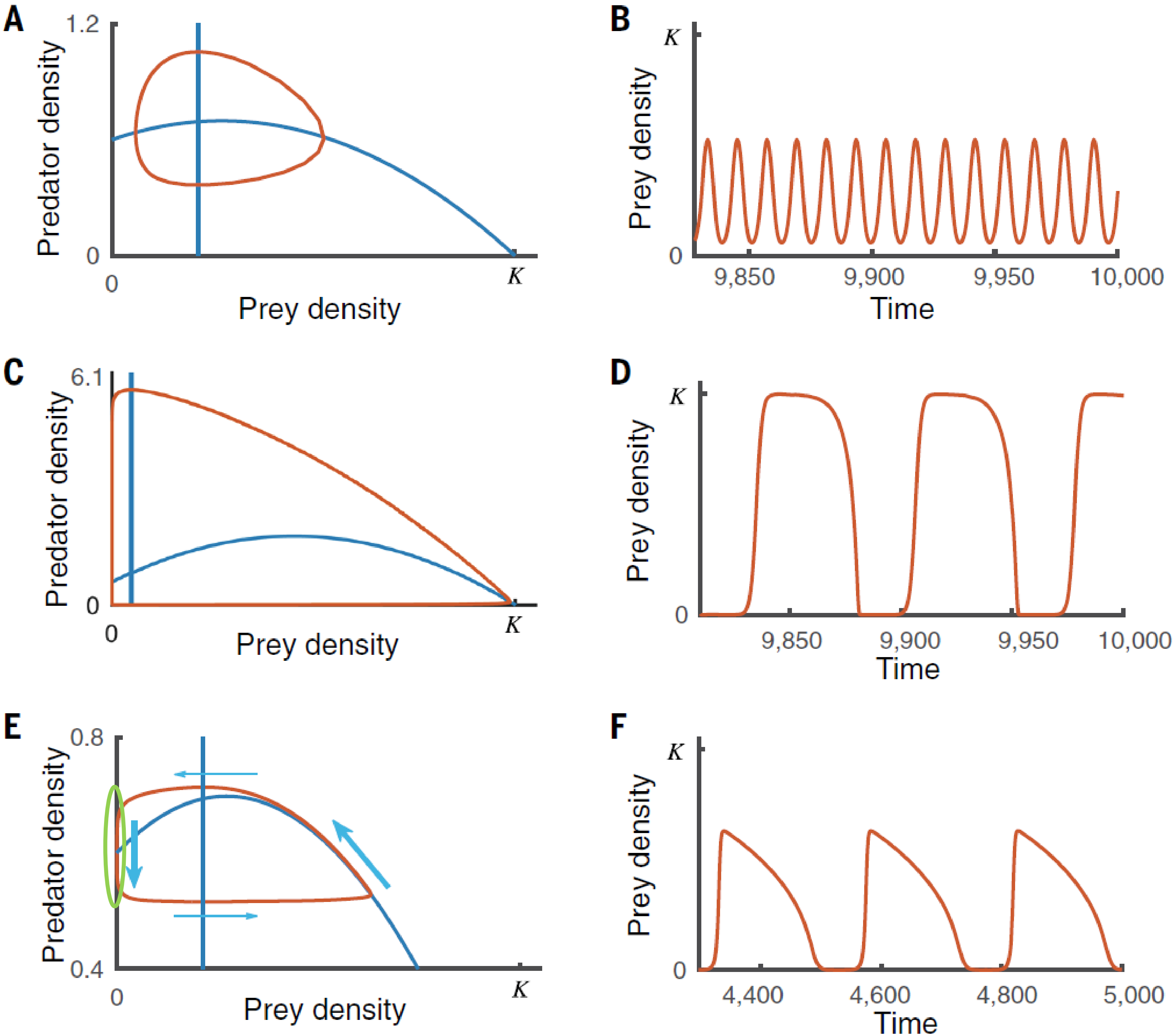


This one has a crawl-by – it gets close to the saddles


A
1.2
Predator density
0
0
K
Prey density
B
K
Prey density
0
9,850
9,900
9,950
10,000
Time
C
6.1
Predator density
0
0
K
Prey density
D
K
Prey density
0
9,850
9,900
9,950
10,000
Time



Multiple-time scale
dynamics lead to transients

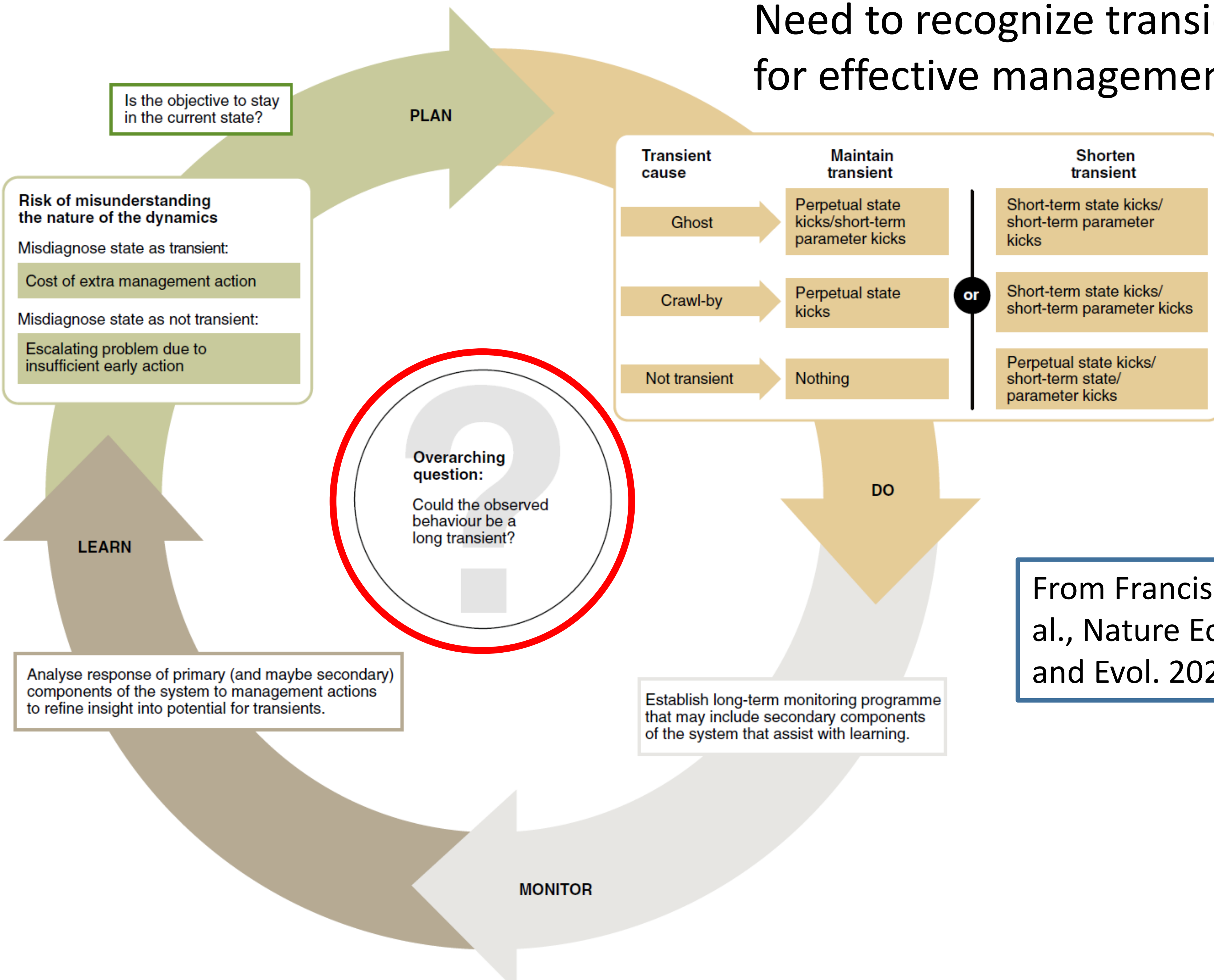


A
1.2
Predator density
0
0
K
Prey density
B
K
Prey density
0
9,850
9,900
9,950
10,000
Time
C
6.1
Predator density
0
0
K
Prey density
D
K
Prey density
0
9,850
9,900
9,950
10,000
Time
E
0.8
Predator density
0.4
0
K
Prey density
F
K
Prey density
0
4,400
4,600
4,800
5,000
Time

For each type of transient we have an empirical example

Type of LT	Relationship to invariant set	Relationship to bifurcation	Dynamics mimicked by LT	Possibility of recurrent LTs?	Biological example
Ghost (Fig. 2)	No invariant set	Occurs past a bifurcation where stable equilibrium is lost	Equilibrium, cycles, chaos	No	Forage fish (*27*) (Fig. 3B)
Crawl-by (Fig. 3, C and D)	Caused by saddle-type invariant set	None necessary	Equilibrium, cycles, chaos	Yes	Phytoplankton-grazer models (*26*)
Slow-fast systems (Fig. 3, E and F)	None necessary	Multiple time scales	Periodic or aperiodic cycles	Yes, if invariant set(s) present	Univoltine insects (*2*) (Fig. 3C)
High dimension (e.g., time delays, space) (Fig. 4A)	None necessary	None necessary	Equilibrium, cycles, chaos	Yes	Chemostat microbial communities (*57*)
Stochasticity (Fig. 4B)	If invariant set present:	None necessary	Aperiodic cycles, chaos	Yes	*Cancer* crabs (*53*)
	If invariant set absent:	Past a bifurcation where cycles/chaos are lost	Quasi-periodic cycles		

Need to recognize transients for effective management



From Francis et al., Nature Ecol. and Evol. 2021

Cannot overemphasize how important this is for management

- 1) Coral-algal-grazer
- 2) Lake eutrophication
- 3) Lake system

But what about stochasticity?

- Simple guess – (almost) everything I said was in the context of deterministic systems, so stochasticity means that transients of more mathematical than biological importance?

But what about stochasticity?

- Simple guess – (almost) everything I said was in the context of deterministic systems, so stochasticity means that transients of more mathematical than biological importance?
- Much more complex than that!
- Hastings et al., 2021 (submitted)

Two simple examples give hints about possibilities

- First, think of salmon, where almost all individuals reproduce the same year
- Start with almost all individuals in the same (single) year class
- The system will slowly approach a stable age distribution

Two simple examples give hints about possibilities

- First, think of salmon, where almost all individuals reproduce the same year
- Start with almost all individuals in the same (single) year class
- The system will slowly approach a stable age distribution
- But with stochasticity this will happen faster – so stochasticity reduces the length of a transient

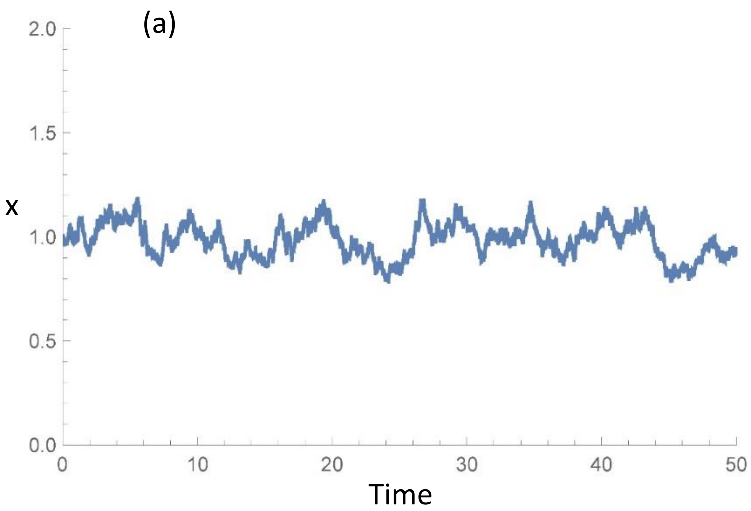
Second example is a simpler version of one we have seen

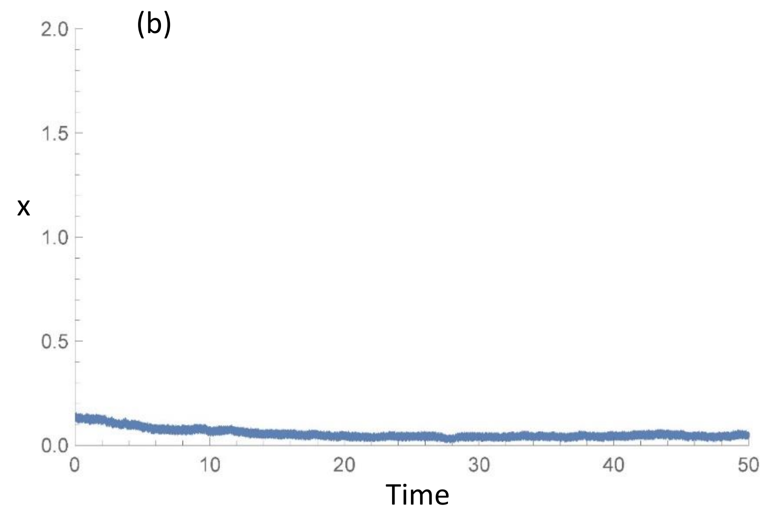
- Think of a predator prey system where deterministically, the system (slowly) approaches a stable equilibrium in an oscillatory fashion.
- Then, add environmental stochasticity to the system -- as shown long ago by Gurney and Nisbet, the system will look exactly like one with deterministic cycles, essentially an arbitrarily long transient.

Effect of stochasticity can depend on level of stochasticity

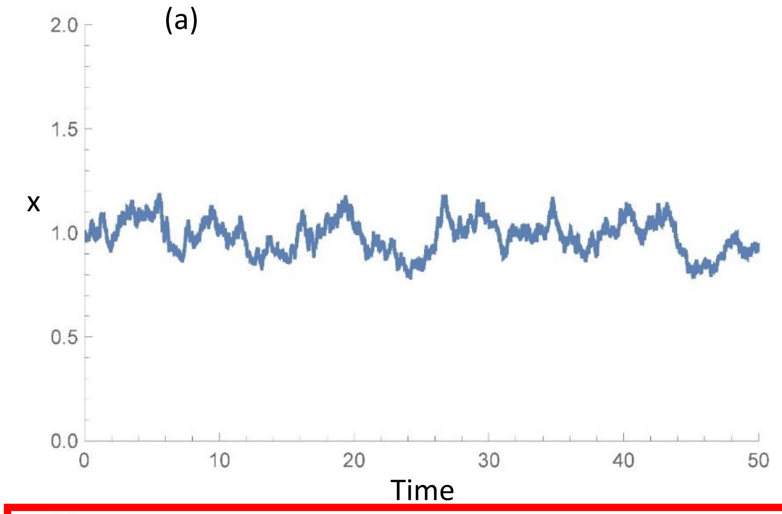
- Look at simplest bistable ecological system – single species with Allee effect
- $\frac{dx}{dt} = x(x - 0.3)(1 - x) + 0.01$
- Scaled population size, small immigration term prevents extinctions
- Deterministic system has two equilibria near 0 and near 1

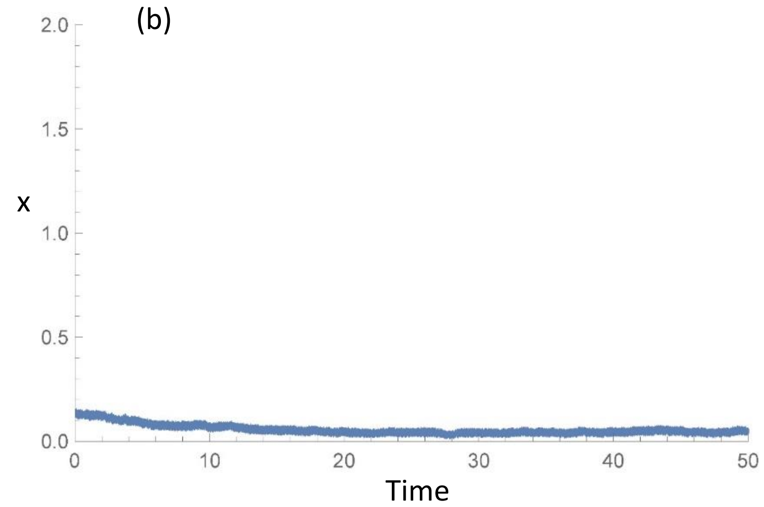
Small stochastic effect is like deterministic system

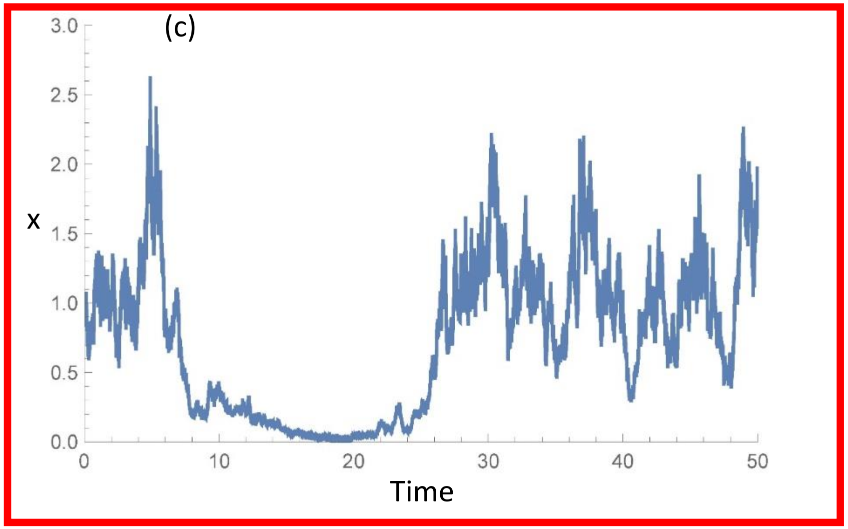




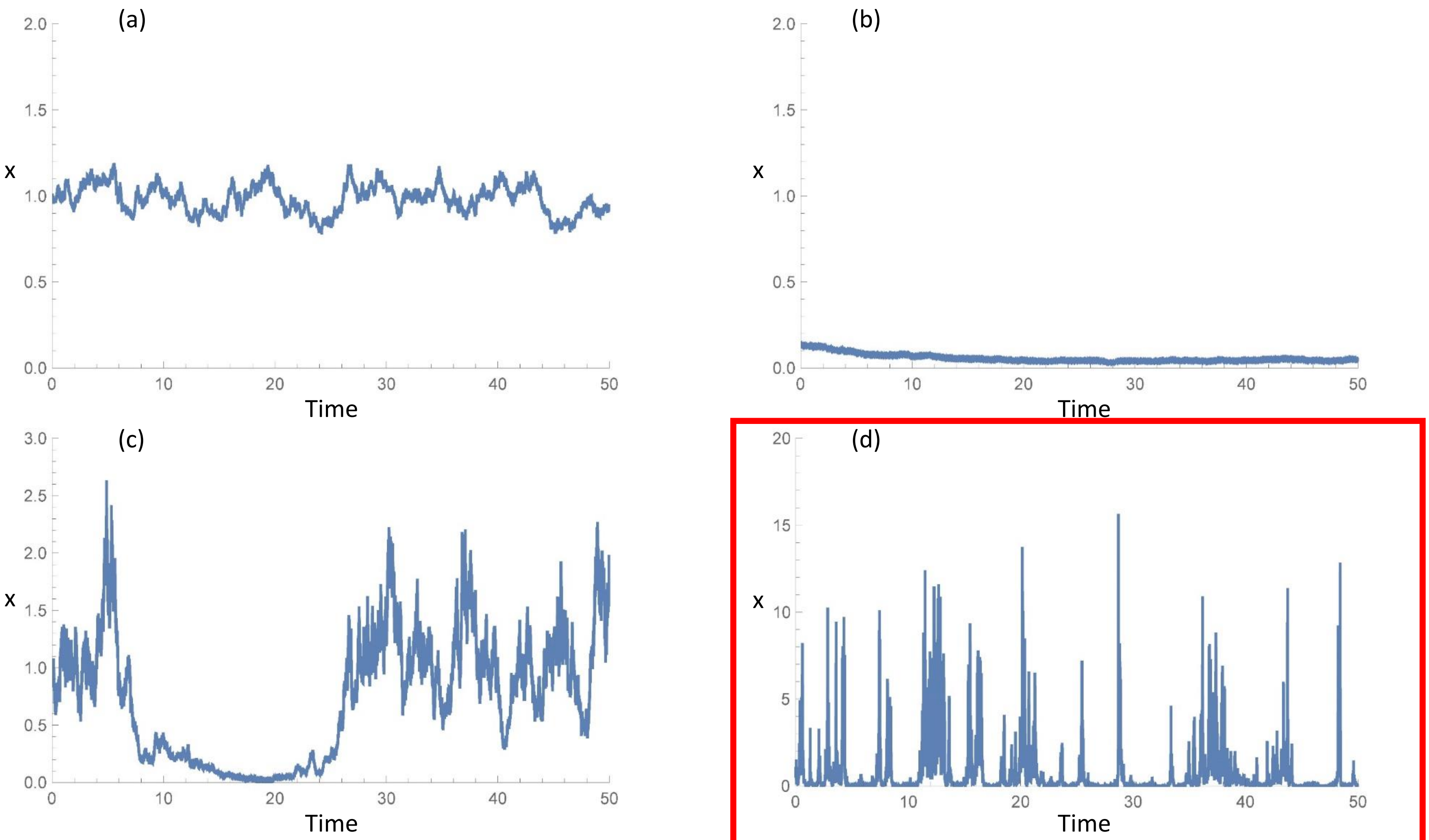
Intermediate stochastic effect is produces transients







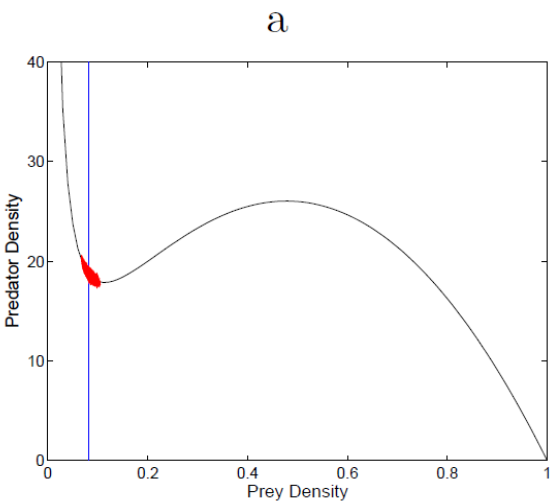
Large stochastic effect is just noise

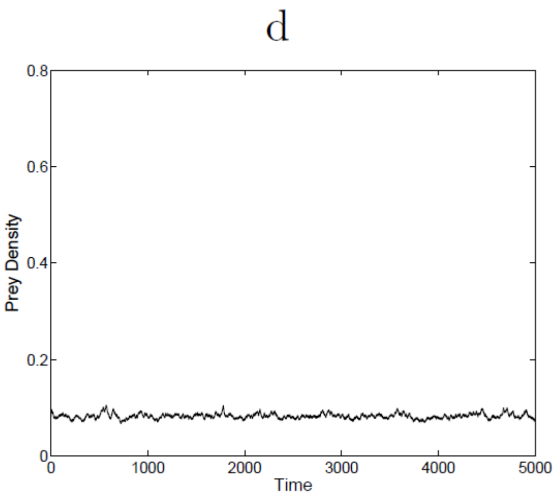


“Excitable systems” show another effect of noise level

- Example is predator-prey model with Holling type 3 systems

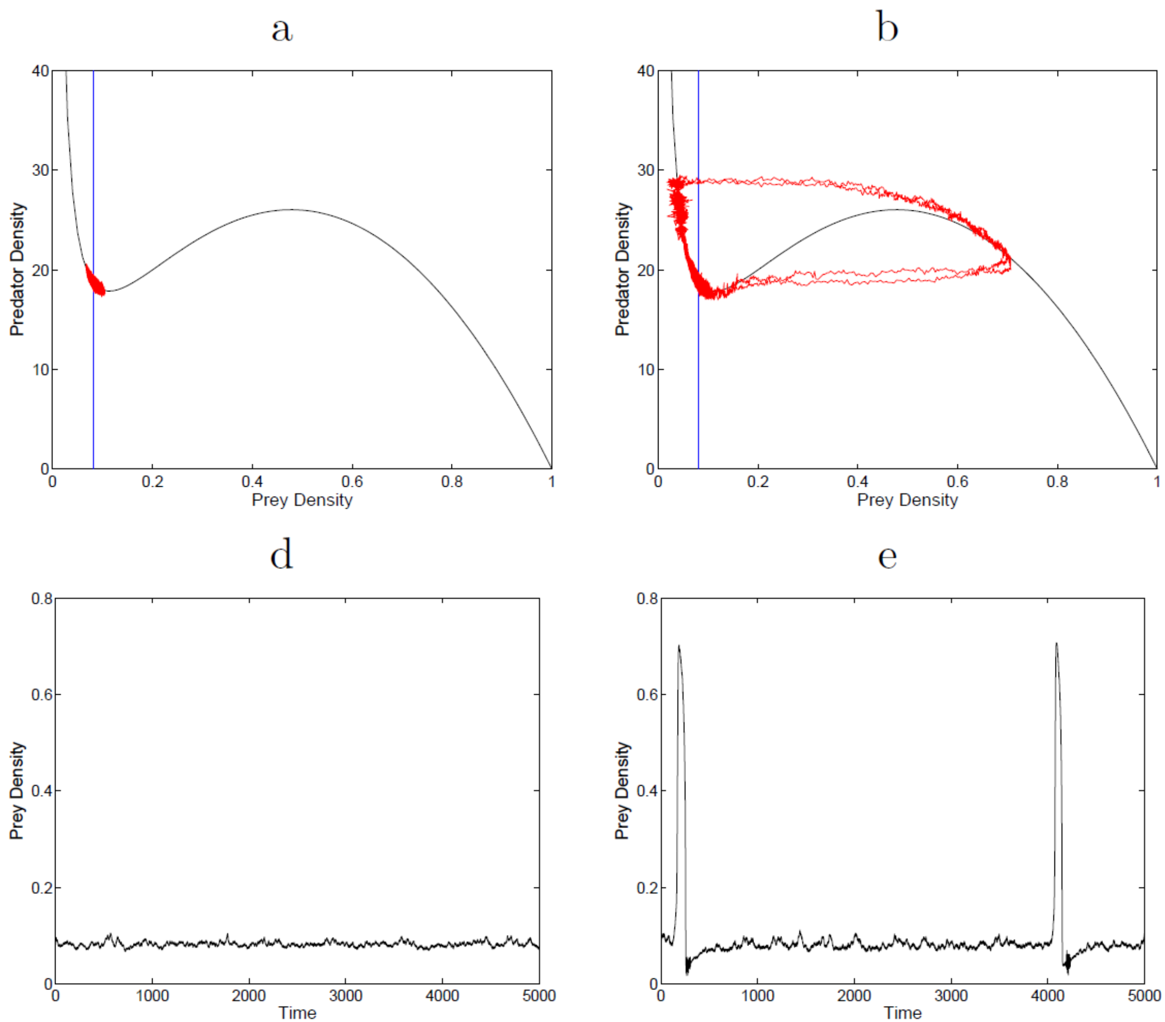
Stochasticity can produce a long transient (predator-prey model with Holling type 3)





Small noise

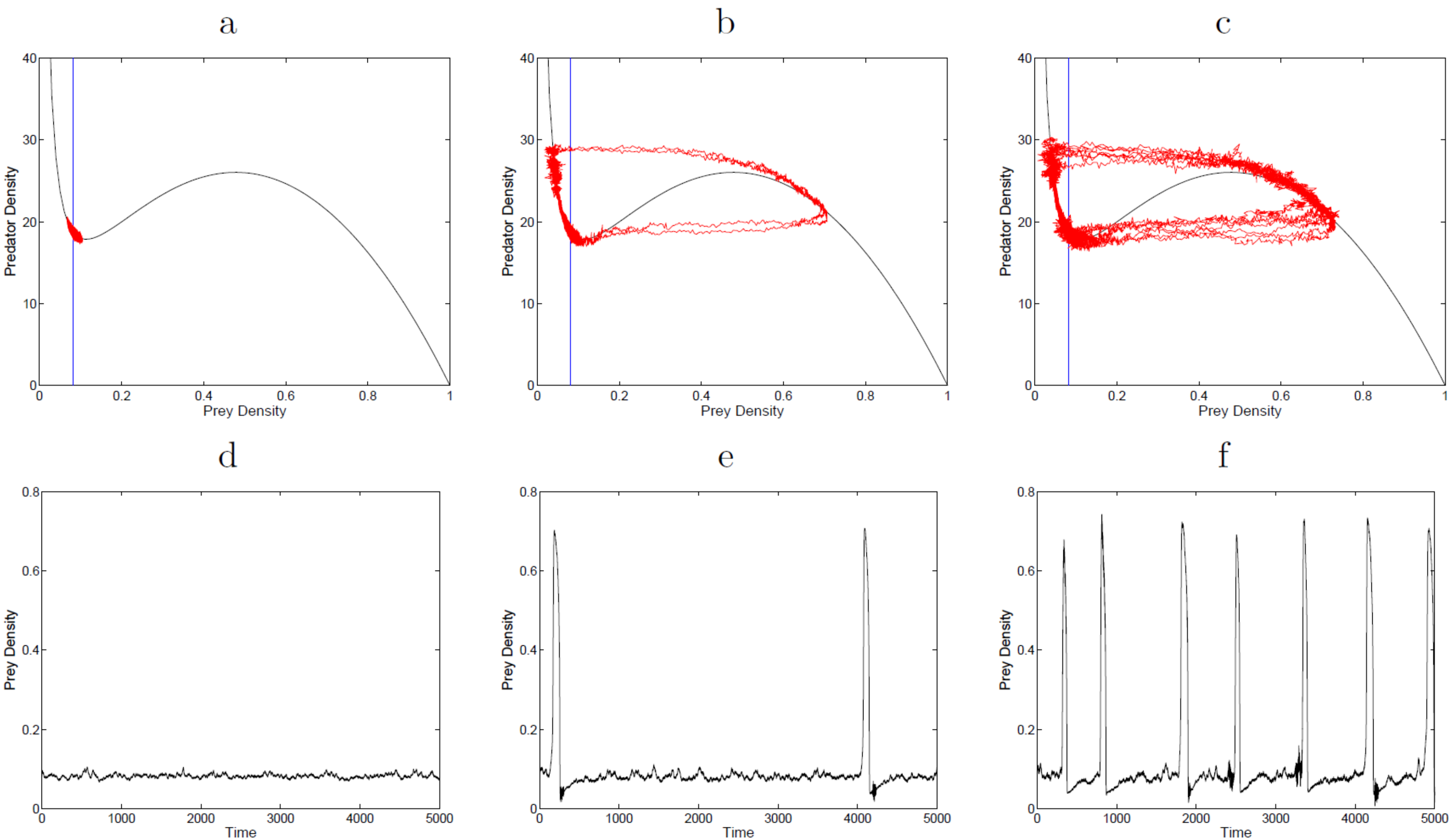
Stochasticity can produce a long transient (predator-prey model with Holling type 3)



Small noise

Intermediate noise

Stochasticity can produce a long transient (predator-prey model with Holling type 3)



Small noise

Intermediate noise

Large noise

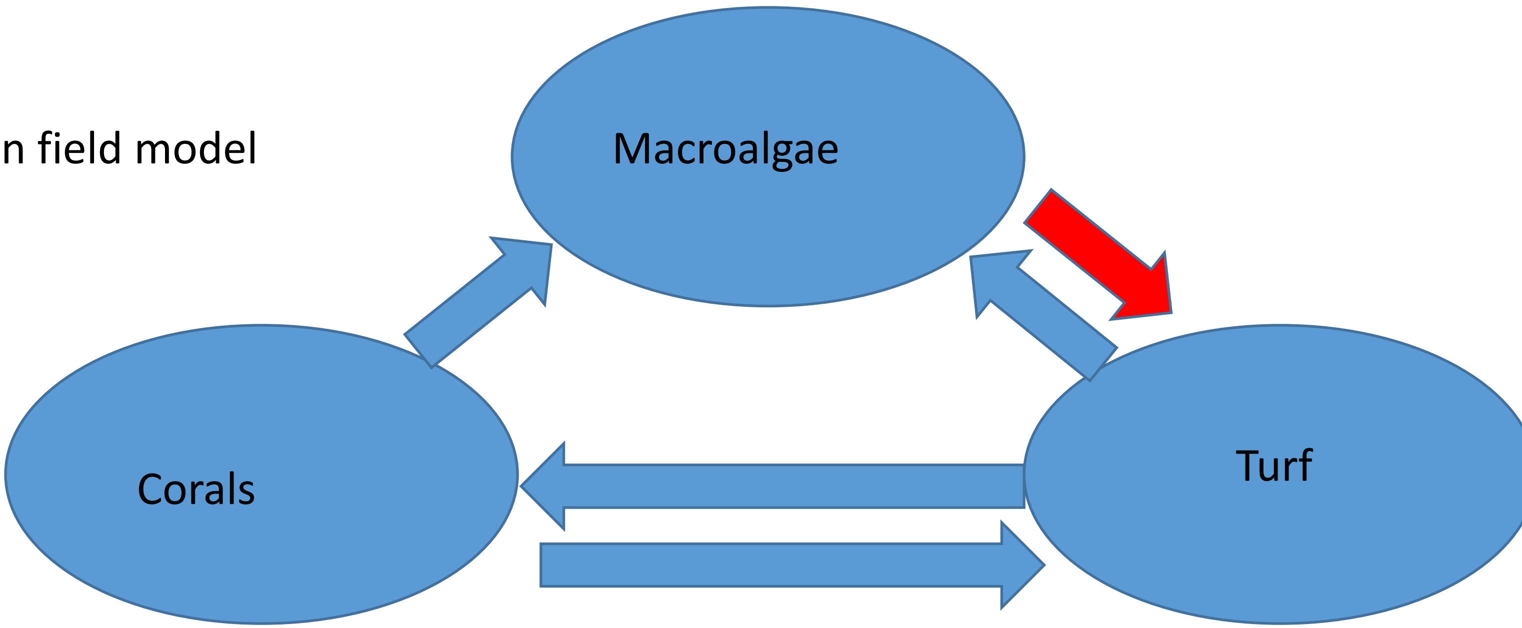
Many more complex interactions possible

- Role of chaotic invariant sets that are no longer attractors
- Other forms of noise (flow-kick) that would include correlation

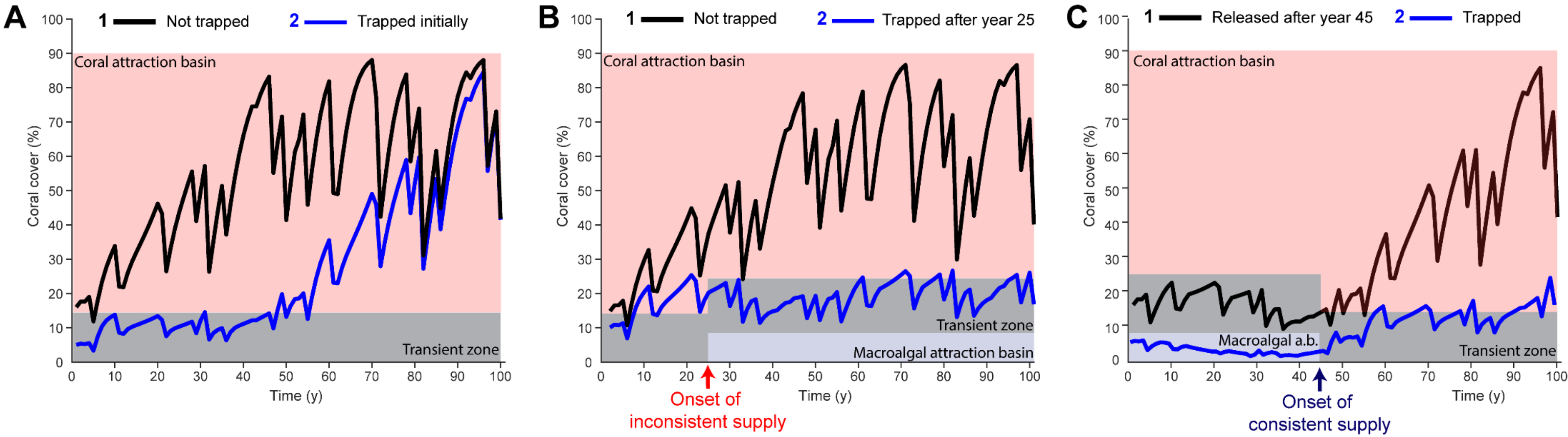
Clearly stochasticity and transients play a role in managment

Grazing a key driver for corals

Use mean field model



- Transient dynamics can mask reef resilience by trapping the system in a state with low recovery rate.



Transient dynamics mask the resilience of coral reefs (submitted)

Karlo Hock[1,2*], Alan Hastings[3], Christopher Doropoulos[4], Russell C. Babcock[4], Juan C. Ortiz[5], Angus Thompson[5], Peter J. Mumby[1,2]

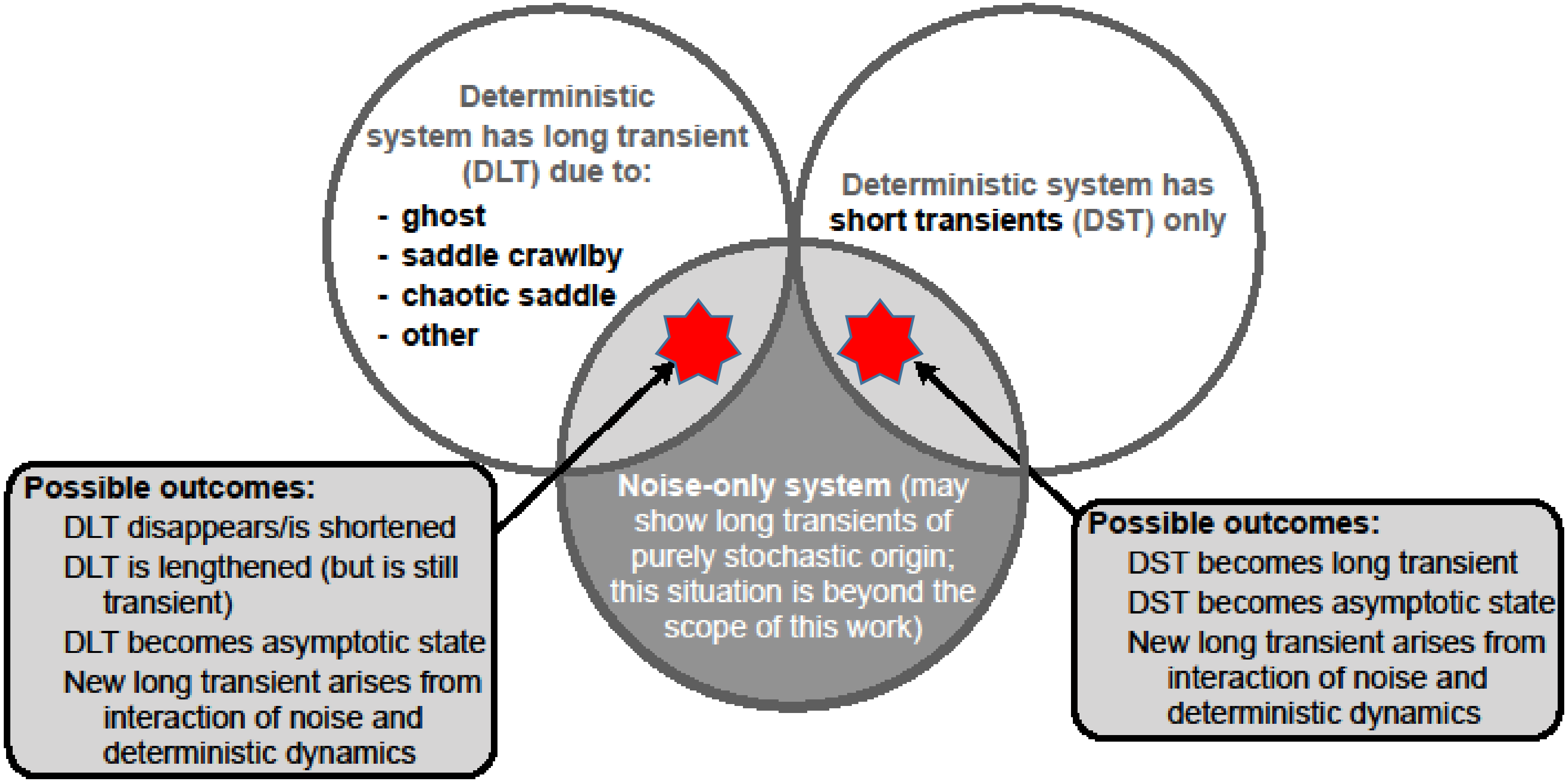
Continuing challenge is to develop an understanding of ecological dynamcis on realistic time scales

Simple model that is deterministic and has no explicit dependence of parameters on time

$$\frac{dx}{dt} = f(x, y)$$
$$\frac{dy}{dt} = g(x, y)$$

Stable equilibrium

"Natural" ecological system



- Real world dynamics fall into the two regions with the red stars, where deterministic and stochastic processes interact.
- DLT = deterministic long transient (i.e. a long transient that exists in the deterministic part of the dynamics); DST = deterministic short transient.

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