Transient Dynamics in Ecology

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Understanding time scales is key for many socio-ecological problems

A typology of time-scale mismatches and behavioral interventions to diagnose and solve conservation problems

Robyn S. Wilson,*¶ David J. Hardisty,† Rebecca S. Epanchin-Niell,‡ Michael C. Runge,§ Kathryn L. Cottingham,** Dean L. Urban,†† Lynn A. Maguire,†† Alan Hastings,‡‡ Peter J. Mumby,§§ and Debra P.C. Peters***

42
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Identify the problem

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

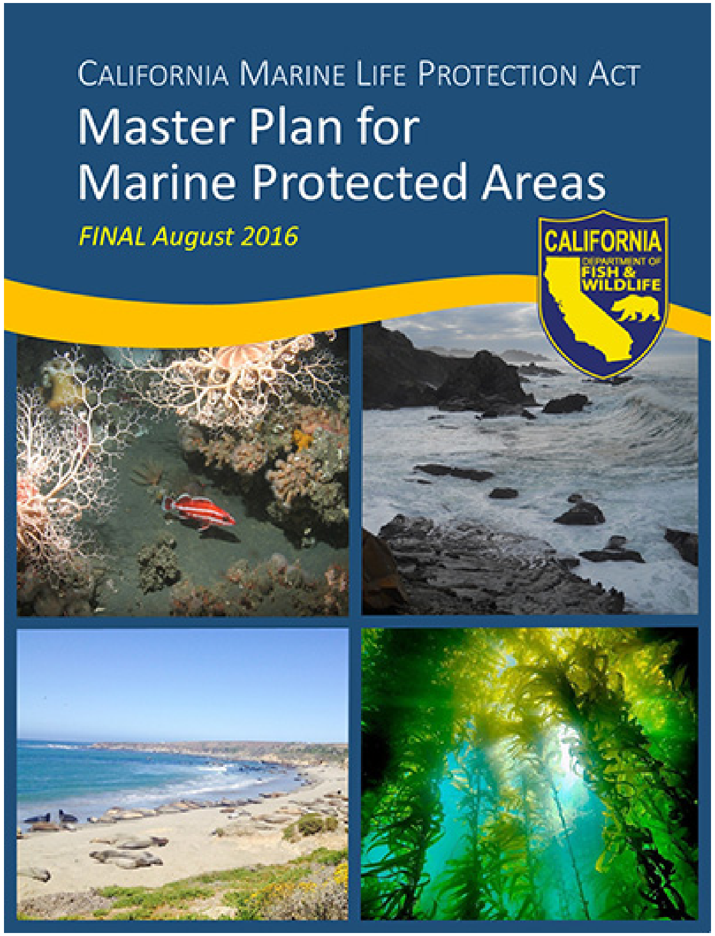
Time scale of ecological response?

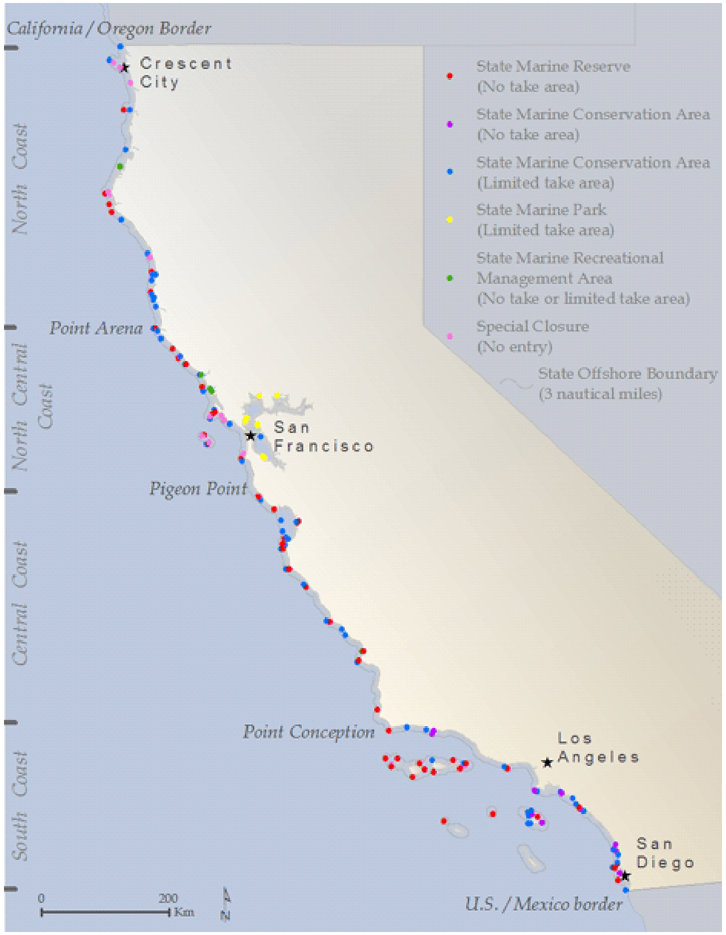
- Marine protected areas have been implemented in California (and around the world)
- Can we say that they are working?

Transient responses of fished populations to marine reserve establishment

J. Wilson White[1], Louis W. Botsford[2], Alan Hastings[3], Marissa L. Baskett[3], David M. Kaplan[4], & Lewis A.K. Barnett[3]

Conservation Letters **6** (2013) 180–191





Problem setup is simple

- Approximate the nonlinear (density dependent) dynamics by a linear model

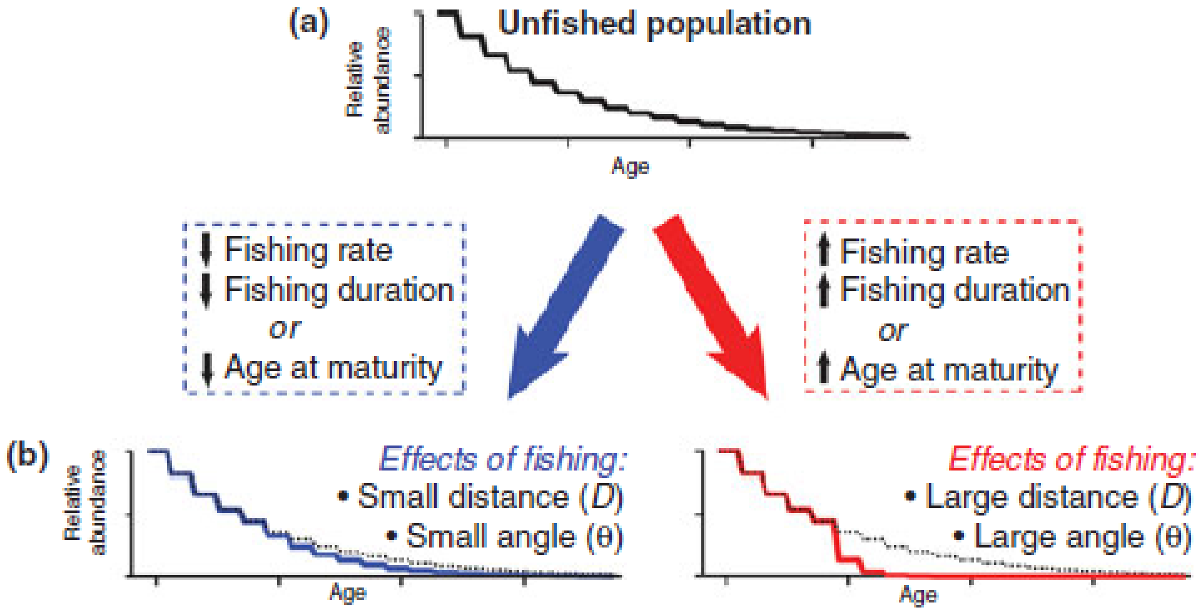
$$\mathbf{N}_{t+1} = \mathbf{A}\mathbf{N}_t$$

$$\mathbf{B} = \lim_{t \to \infty} \frac{\mathbf{A}^t}{\lambda_1^t} = \frac{\mathbf{w}_1 \mathbf{v}_1'}{\mathbf{v}_1 \mathbf{w}_1'}$$

$$\lim_{t \to \infty} \mathbf{A}_0^t \mathbf{N}_0 \propto \mathbf{B}\mathbf{N}_0 \propto \mathbf{w}_1$$

Important to develop general principles of response

- Time scale of response depends on state of perturbed (fished) system; starting point is how far the system is from a stable age distribution



Approach now being used to develop monitoring plan for MLPA marine reserves – challenges of data-model interface

- Kaplan et al Ecological Applications in press
- Yamane et al submitted
- Using models to explain response over realistic time scales using age structure and estimates of fishing pressure

Even 'linear' 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

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

Dispersal kernel

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

$D = 800$

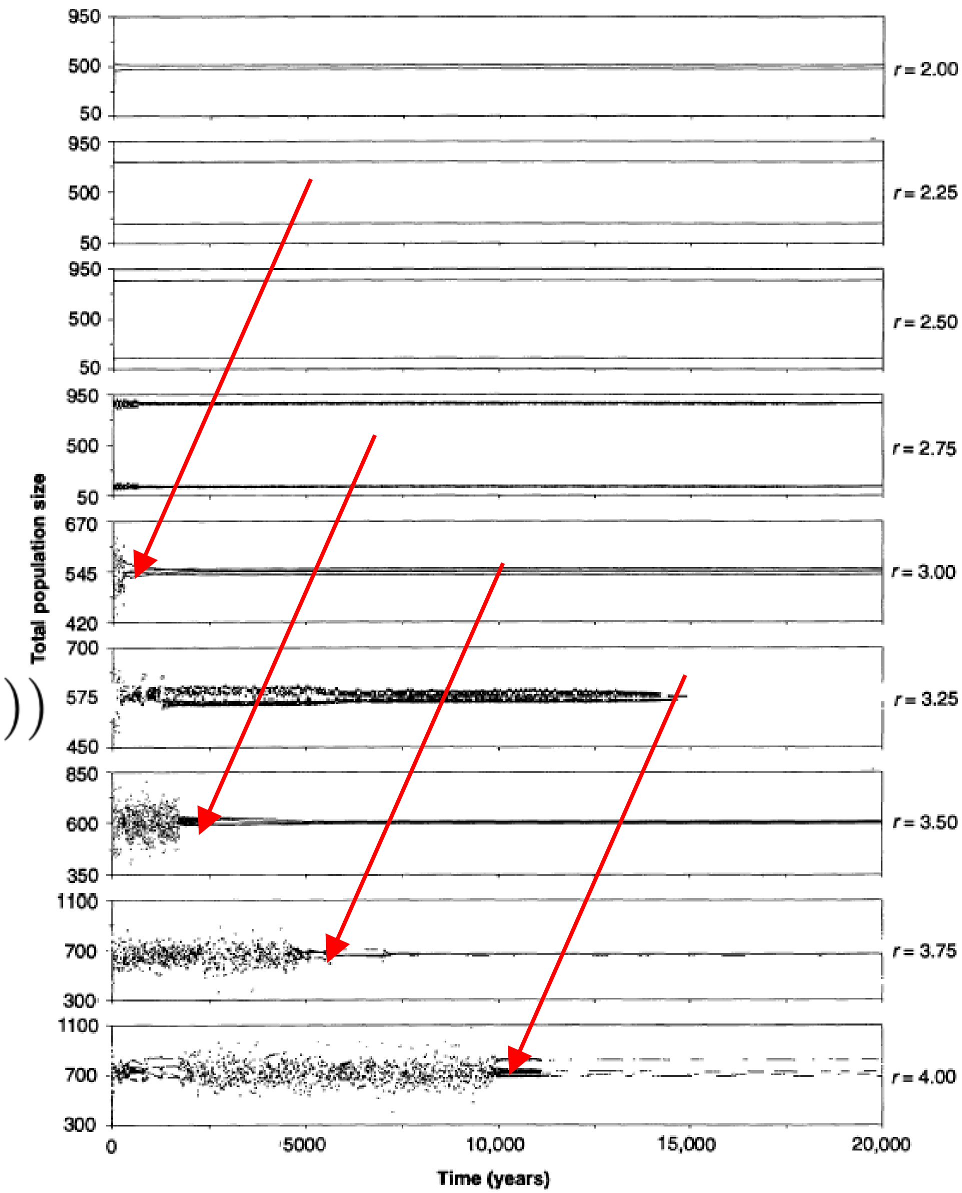


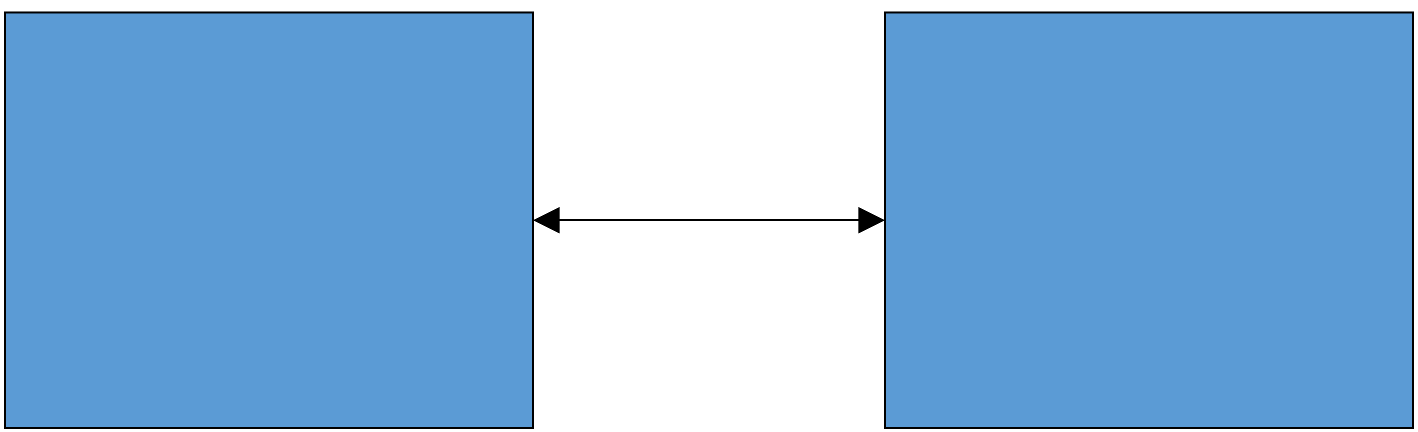
Fig. 1. Dynamics of a spatially structured model (1–3) of a population with pelagic larvae along a coastline as a function of the growth rate r. In all cases, the initial conditions were chosen randomly in space from a uniform distribution, and $D = 800$. The presence of long transients is apparent from the plots for all values of $r \geq 3.25$.

Two patches, single species
Hastings, 1993, Gyllenberg et al 1993

$$\tilde{x}_i(t) = f[r_i, x_i(t)],$$

$$f(r, x) = rx(1 - x),$$

Alternate growth



Two patches, single species
Hastings, 1993, Gyllenberg et al 1993

$$\tilde{x}_i(t) = f[r_i, x_i(t)],$$

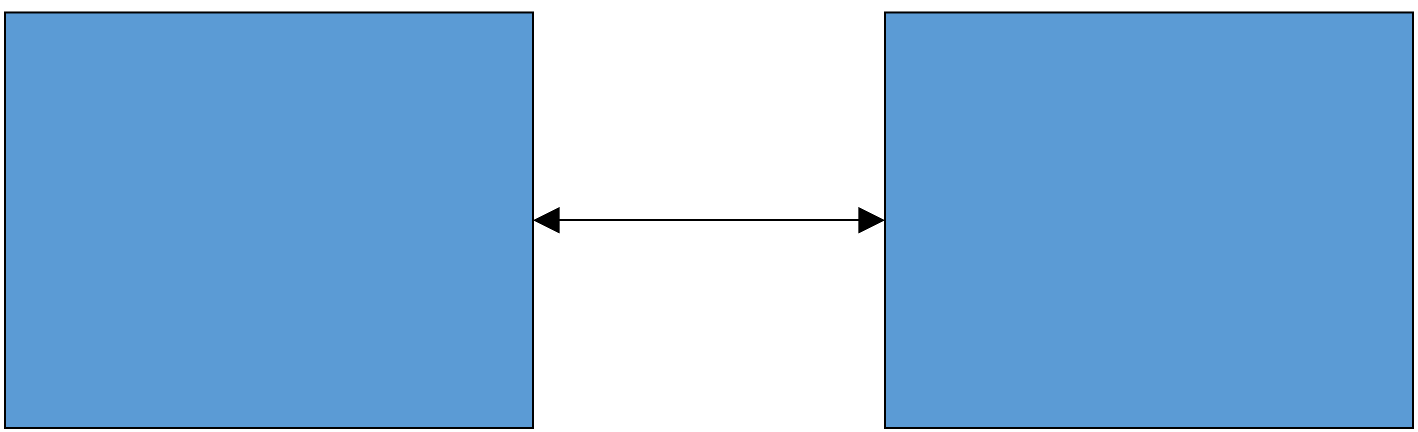
$$f(r, x) = rx(1 - x),$$

Alternate growth

$$x_1(t + 1) = \tilde{x}_1(t) + D[\tilde{x}_2(t) - \tilde{x}_1(t)]$$

$$x_2(t + 1) = \tilde{x}_2(t) + D[\tilde{x}_1(t) - \tilde{x}_2(t)],$$

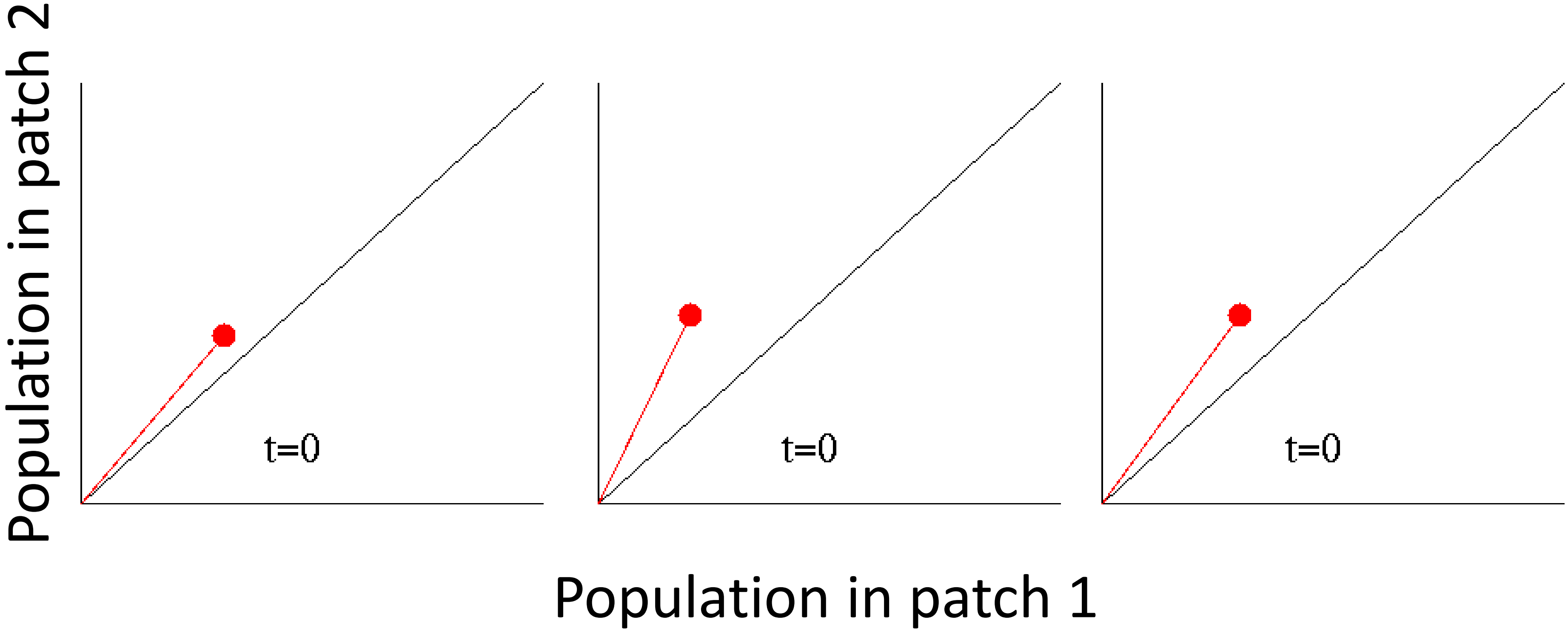
And then dispersal



But what do the dynamics look like on ecologically realistic time scales?

- Choose r=3.8, D=0.15
- Follow population sizes through time for different choices of initial conditions
- Red dot is current population levels, line comes from the previous population levels

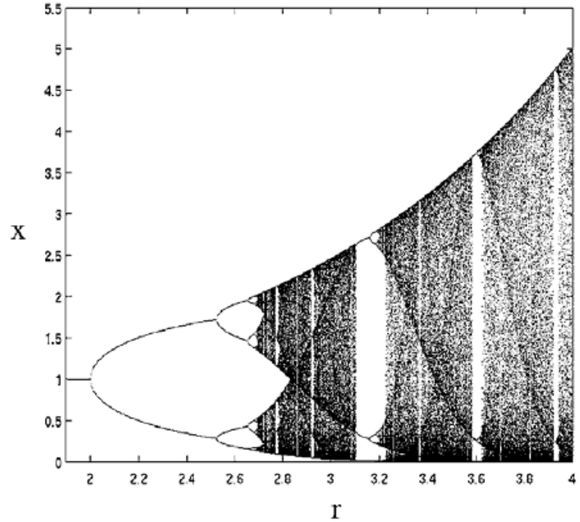
Three different initial conditions



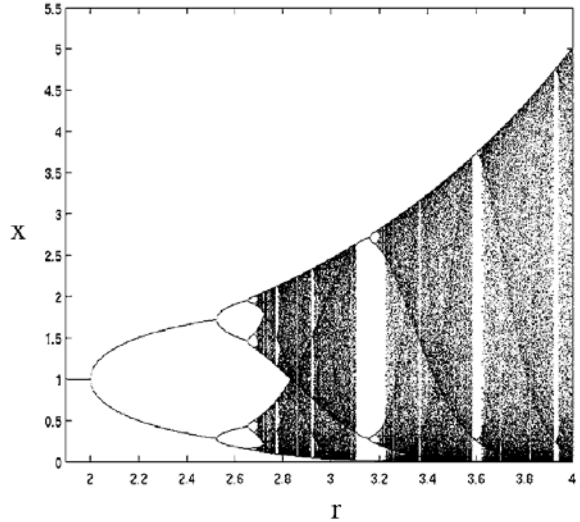
- Two ends of the line represent population in two patches in two successive years; note change between in phase (synchronous, along 45 degree line) and out of phase (across 45 degree line)

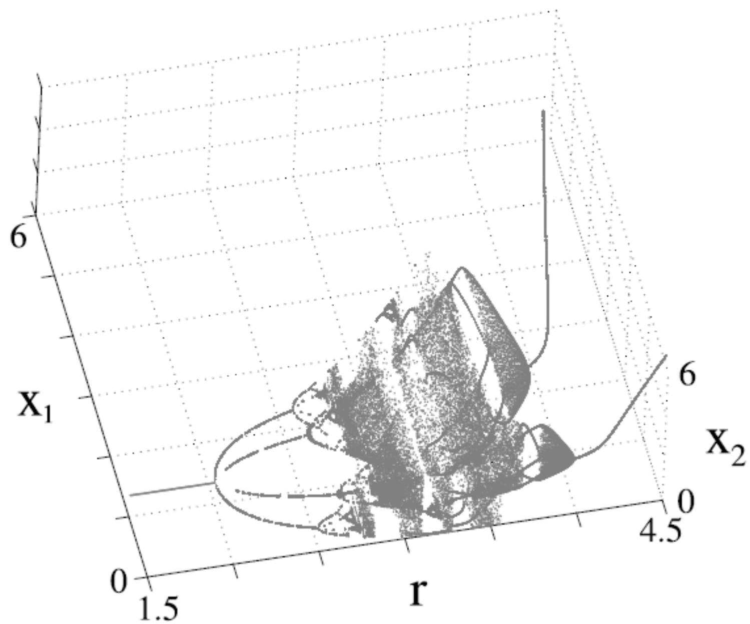
Analytic treatment of transients in coupled patches (Wysham & Hastings, BMB, 2008; H and W, Ecol Letters 2010;) helps to determine when, and how common

- Depends on understanding of crises
  - Occurs when an attractor ‘collides’ with another solution as a parameter is changed
  - Typically produces transients
  - Can look at how transient length scales with parameter values
- Start with 2 patches and Ricker local dynamics

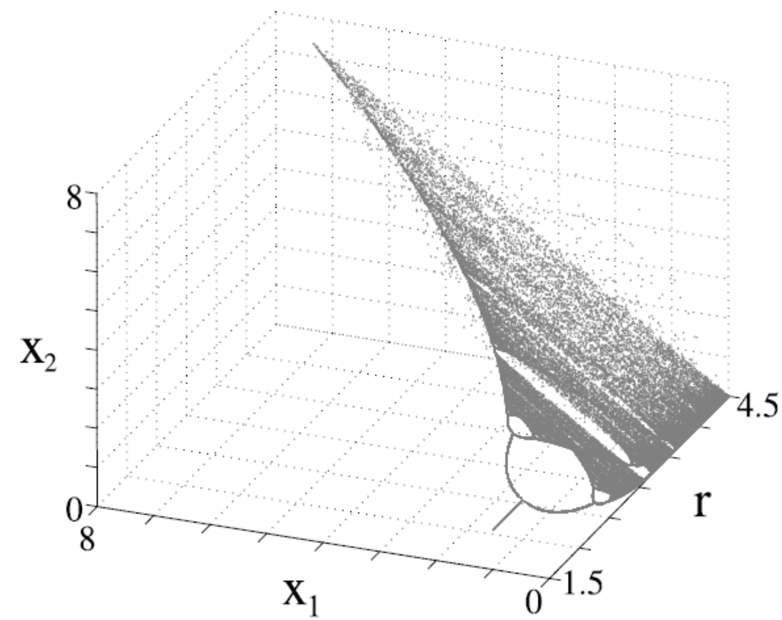


x
r
0
0.5
1
1.5
2
2.5
3
3.5
4
4.5
5
5.5
2
2.2
2.4
2.6
2.8
3
3.2
3.4
3.6
3.8
4



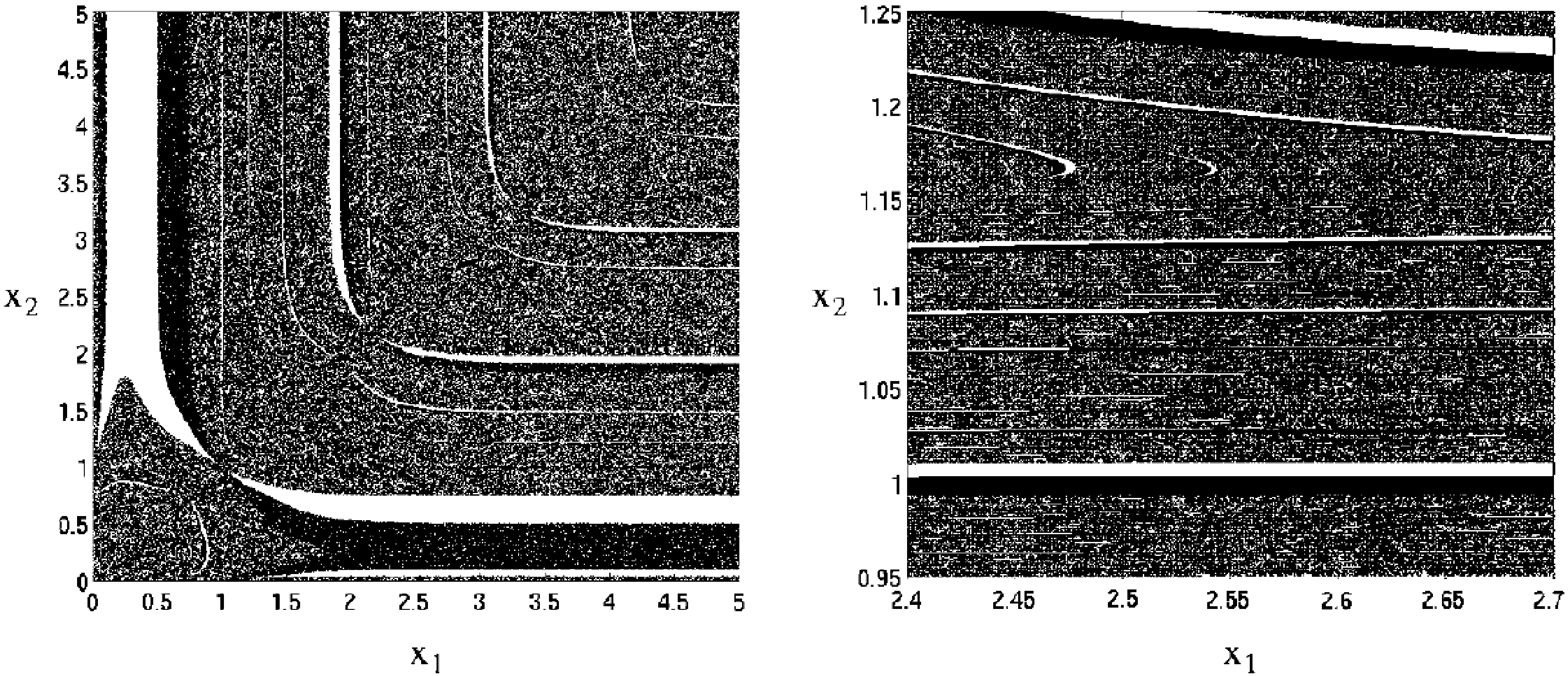


Weak coupling

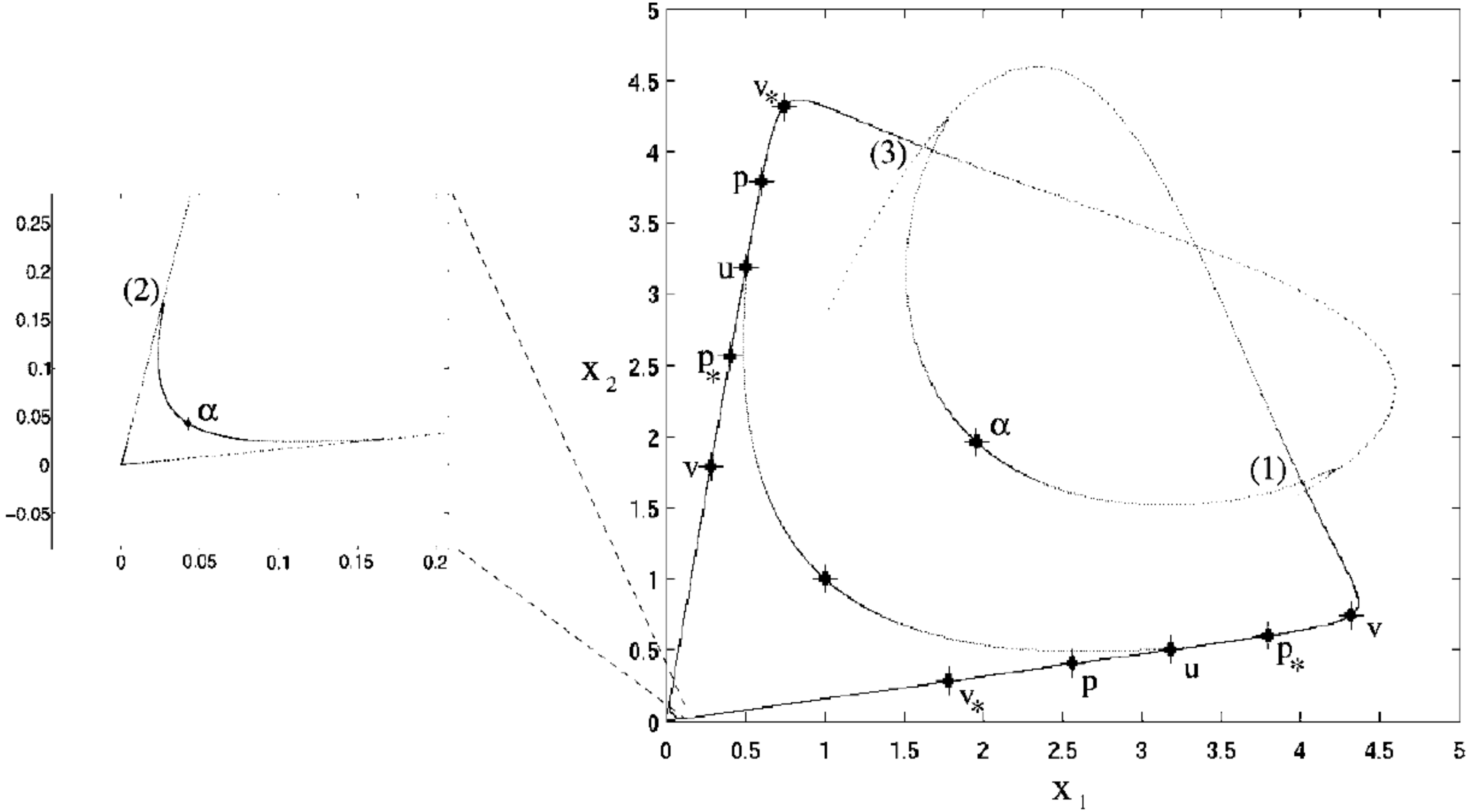


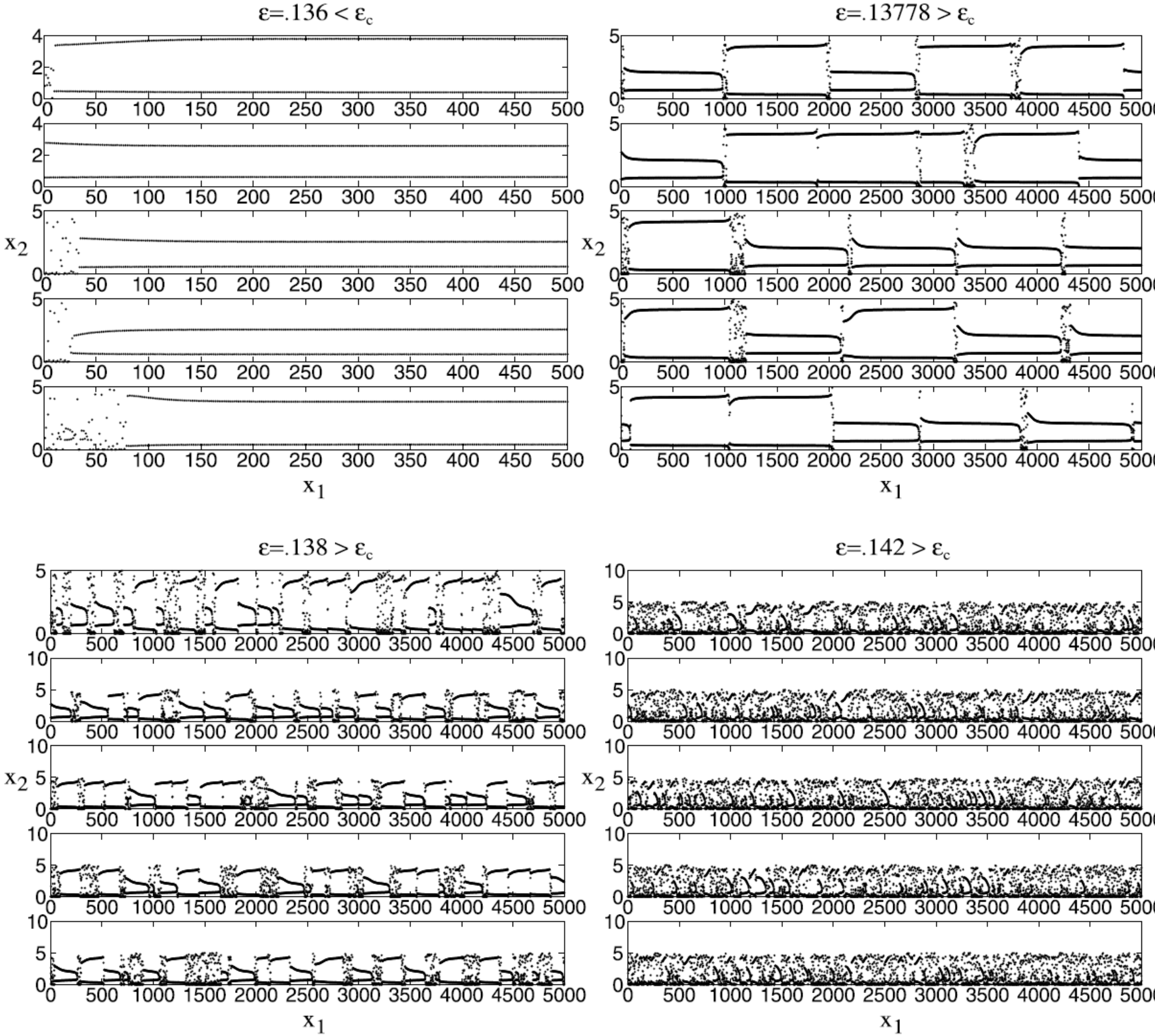
Strong coupling

Entangled basins of attraction



Period 2 orbits, fixed points, and unstable manifolds: multiple heteroclinic connections and one heteroclinic tangle

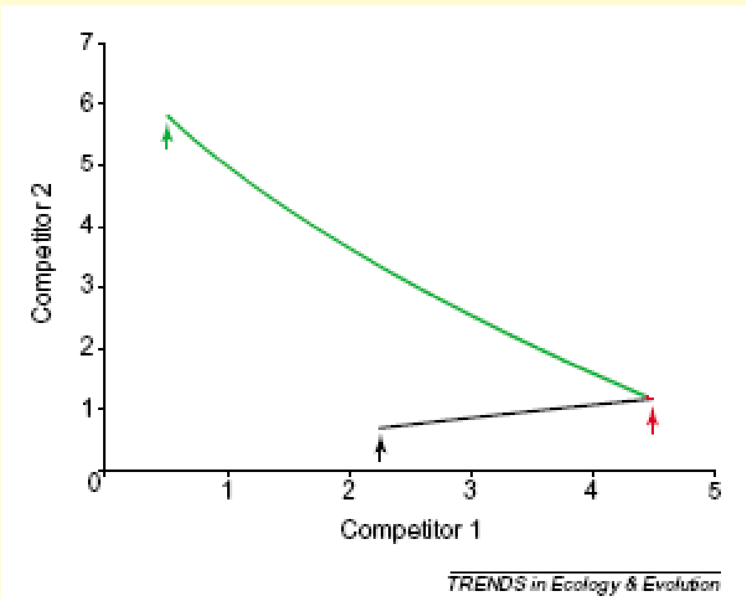




$\varepsilon=.136 < \varepsilon_c$
$\varepsilon=.13778 > \varepsilon_c$
$\varepsilon=.138 > \varepsilon_c$
$\varepsilon=.142 > \varepsilon_c$
x_2
x_1

As a start to understanding --Saddles are a first simple way to approach transients

- Start with simplest example
  - Lotka-Volterra competition
  - Saddle is an equilibrium



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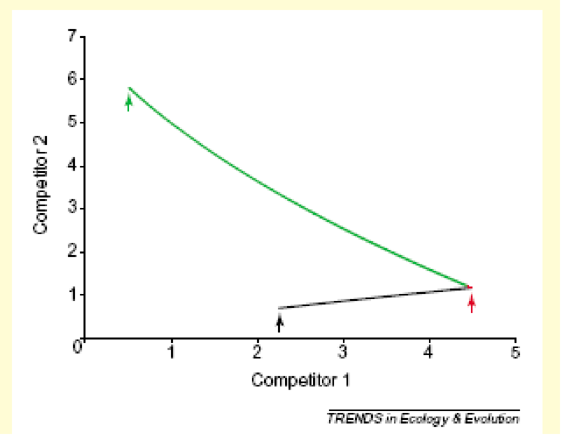
ELSEVIER

Transients: the key to long-term ecological understanding?

Alan Hastings

As a start to understanding --Saddles are a first simple way to approach transients

- Start with simplest example
  - Lotka-Volterra competition
  - Saddle is an equilibrium
- Start at analytic understanding
- Laboratory example
  - Tribolium
  - Saddle is a 2-cycle
- Complex non-spatial model (plankton)



Transient can be important for coexistence

Available online at www.sciencedirect.com
SCIENCE DIRECT
Theoretical Population Biology 64 (2003) 431–438
Theoretical Population Biology
http://www.elsevier.com/locate/ytpbi

Spatial mechanisms for coexistence of species sharing a common natural enemy

Aaron A. King[a,*] and Alan Hastings[b]

Instrinsic growth rate

$$n_j^i(t+1) = \boxed{\lambda_i} N_j^i(t) f_i(P_j(t)),$$

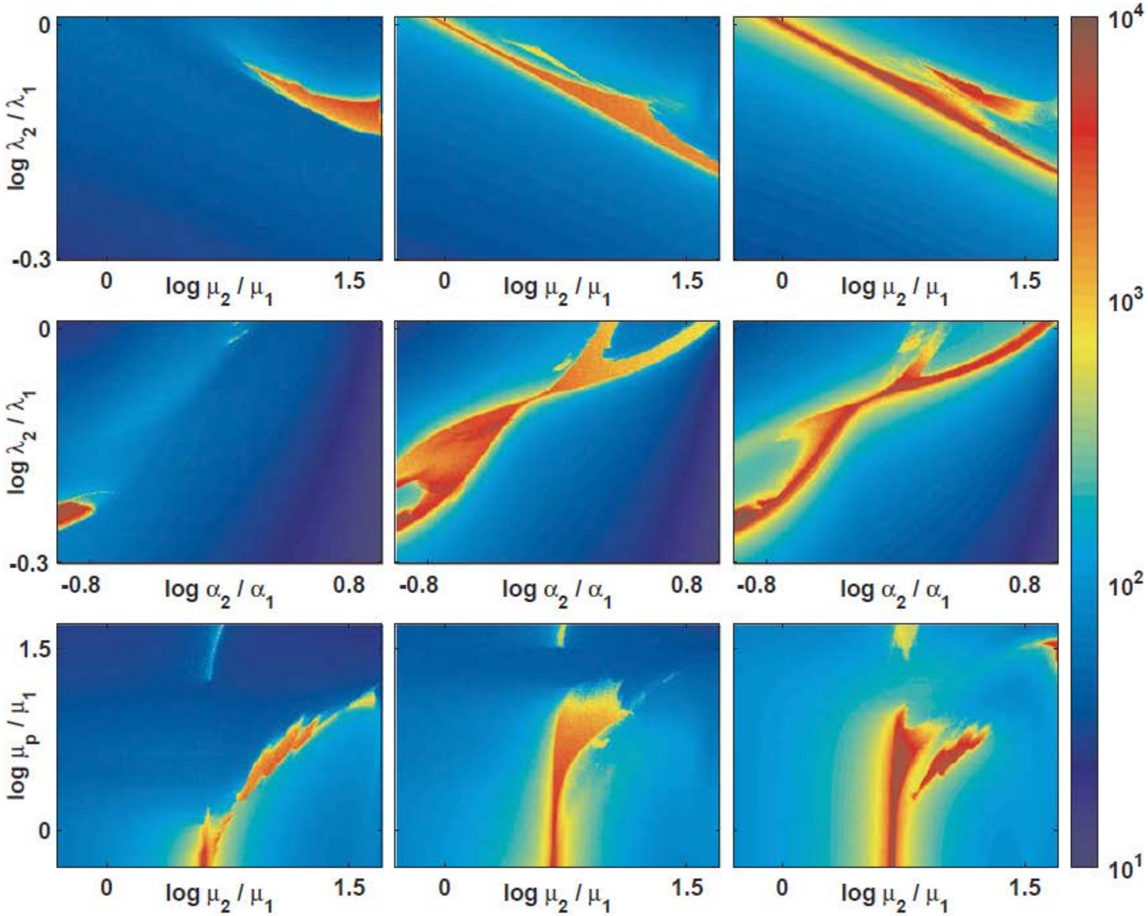
$$p_j(t+1) = \sum_i c_i N_j^i(t)(1 - f_i(P_j(t))),$$

$$f_i(P) = \boxed{\exp(-\alpha_i P).}$$

Probability the host is not parasitized – 0 term in the Poisson distribution

$$\boxed{\begin{aligned} N_j^i(t) &= (1-\mu_i)\, n_j^i(t) + \frac{\mu_i}{M} \sum_k n_k^i(t), \\ P_j(t) &= (1-\mu_p)\, p_j(t) + \frac{\mu_p}{M} \sum_k p_k(t), \end{aligned}}$$

Random movement



- Mean transient coexistence duration. Each row depicts a distinct slice through the six-dimensional parameter space.

Can we make this more systematic?


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

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.

Long transients in ecology: theory and applications

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Tessa Francis
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Gabriel Gellner
Integrative Biology, University of Guelph, Canada

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Sergei Petrovskii*
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Mary Lou Zeeman
Mathematics, Bowdoin College, Brunswick

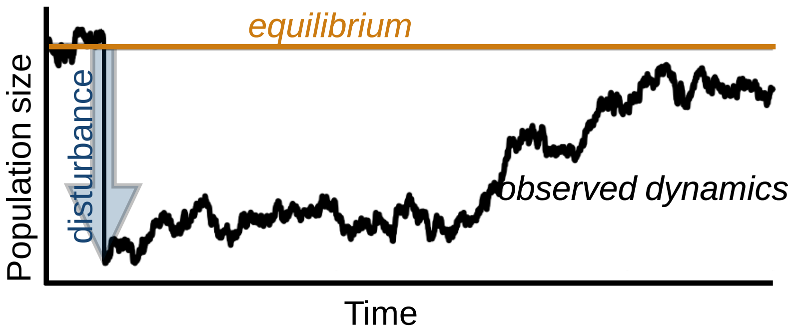
More of the mathematical details are in this manuscript in press in Physics of Life Reviews

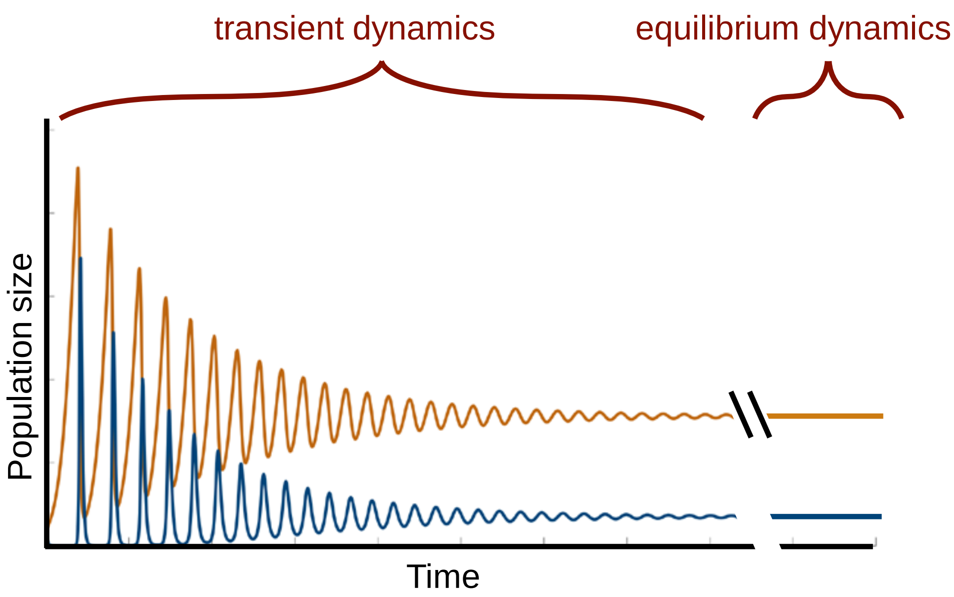
Use ideas from dynamical systems to classify long transients

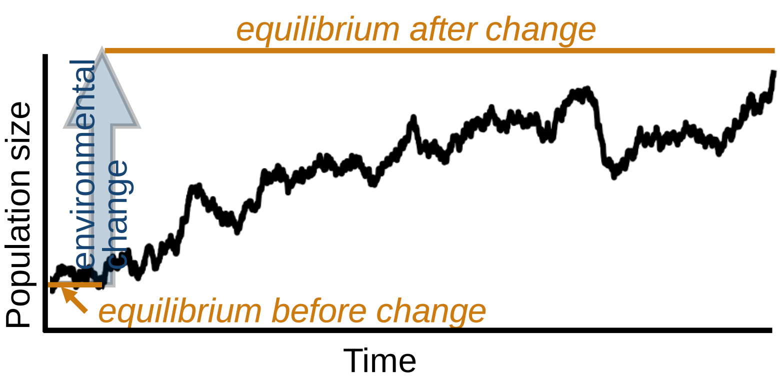
- Show when they will arise

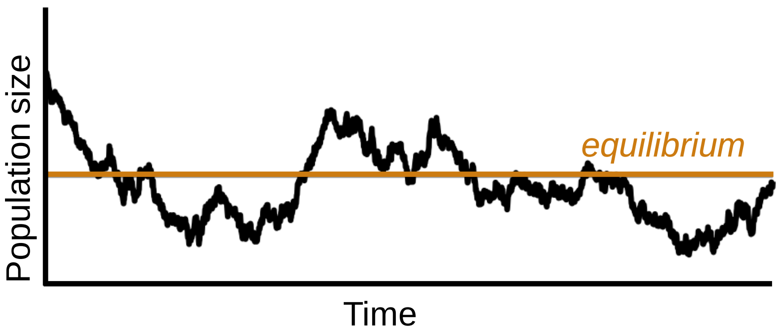
What do we mean by "long transients"?

- 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 a stable equilibrium









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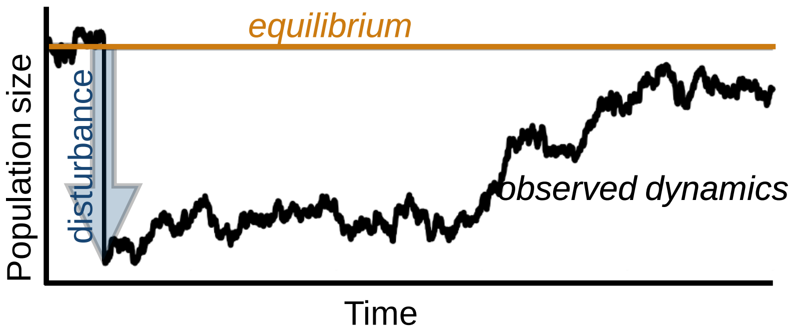

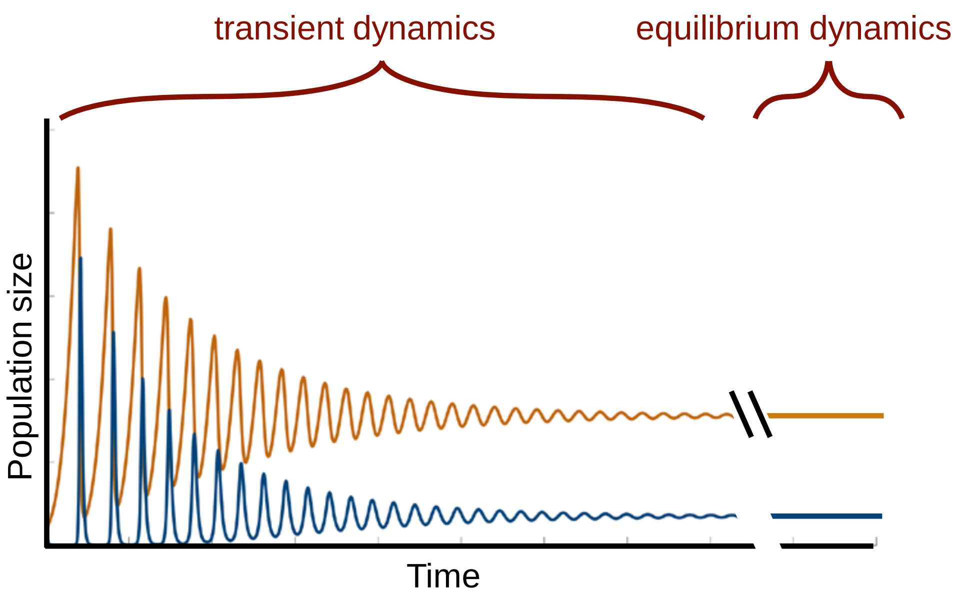

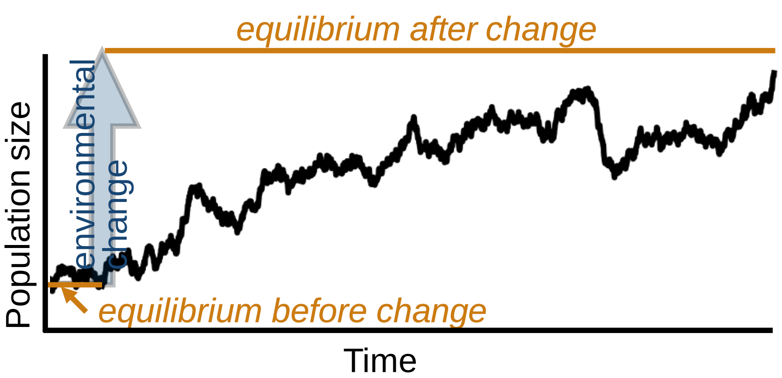

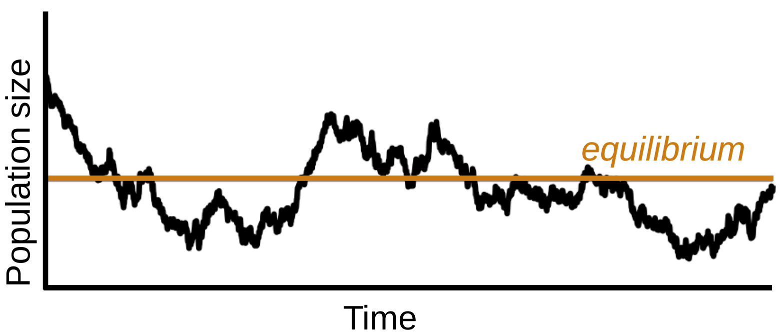

More empirical examples

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

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Transients in *Tribolium*

- Note the flip between relatively constant dynamics and cycles in the replicate on the left, and the cycles in the replicate on the right

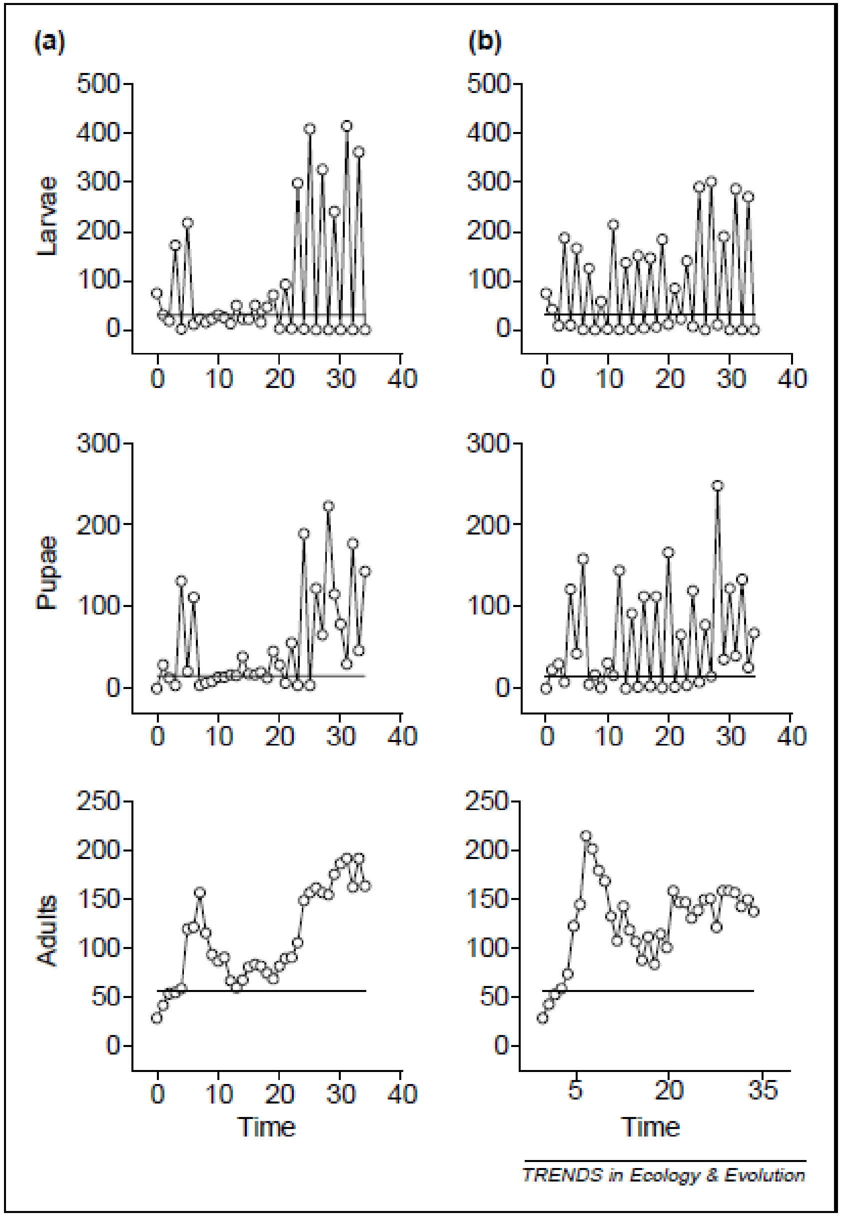
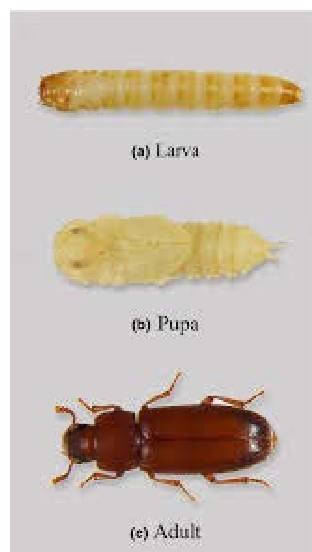


Figure 2. Transient dynamics are shown for a laboratory population of *Tribolium*, as reproduced with permission from [6]. For one replicate **(a)**, the population numbers (of larvae, pupae and adults) go through a period of time of approximate constancy, and then the dynamics change so that a two-point cycle is observed. For the other replicate **(b)**, no transient dynamics are observed. This demonstrates that, even in a simple laboratory system, transient dynamics can be observed and that different dynamics are observed on a different timescale.



Cushing et al. (1998)

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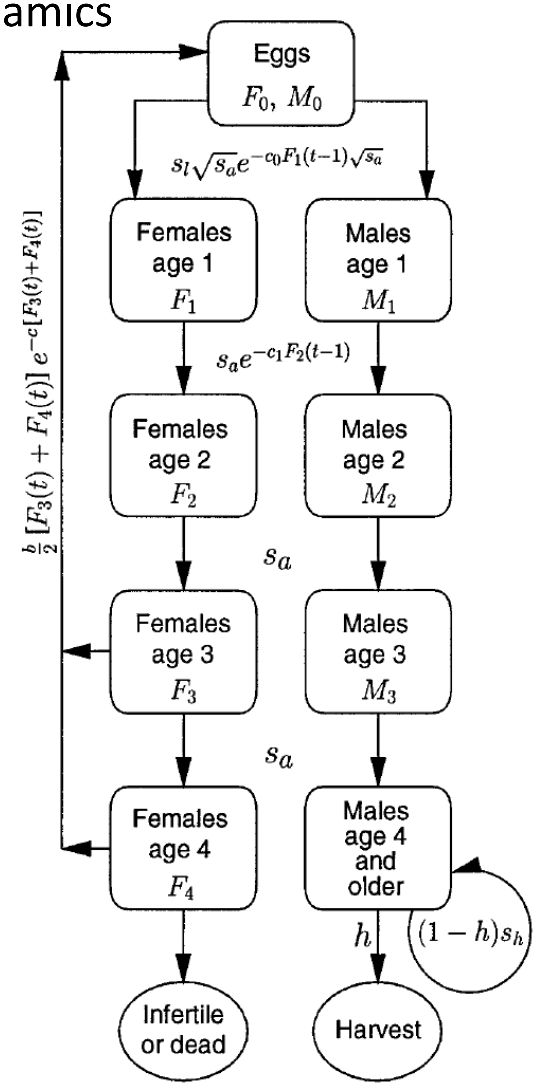
Stochastic Dynamics and Deterministic Skeletons: Population Behavior of Dungeness Crab

Kevin Higgins,* Alan Hastings, Jacob N. Sarvela, Louis W. Botsford

www.sciencemag.org • SCIENCE • VOL. 276 • 30 MAY 1997

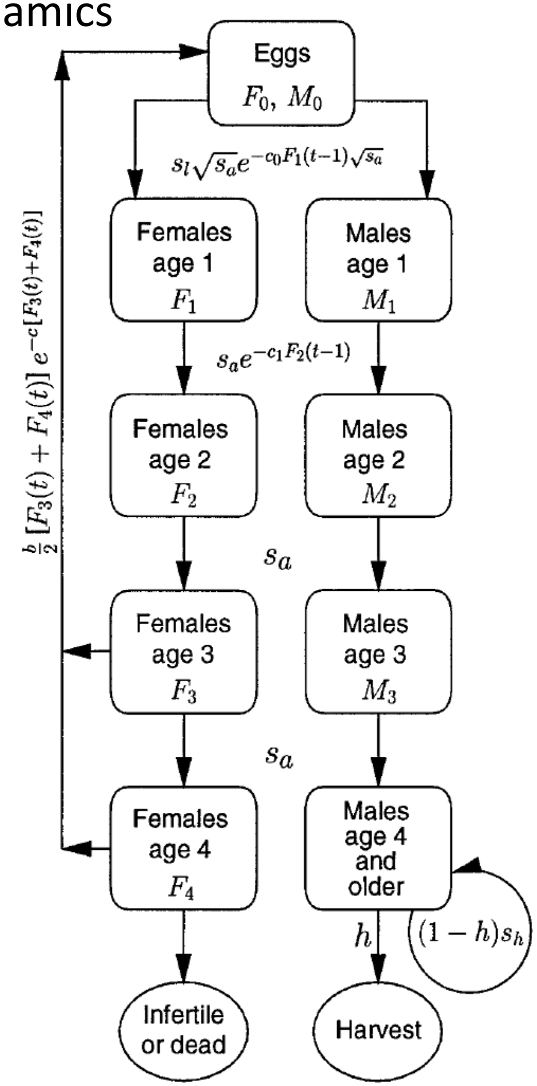
Detailed model of Dungeness crab dynamics



Observe this

Detailed model of Dungeness crab dynamics

Observed harvests and one step ahead predictions



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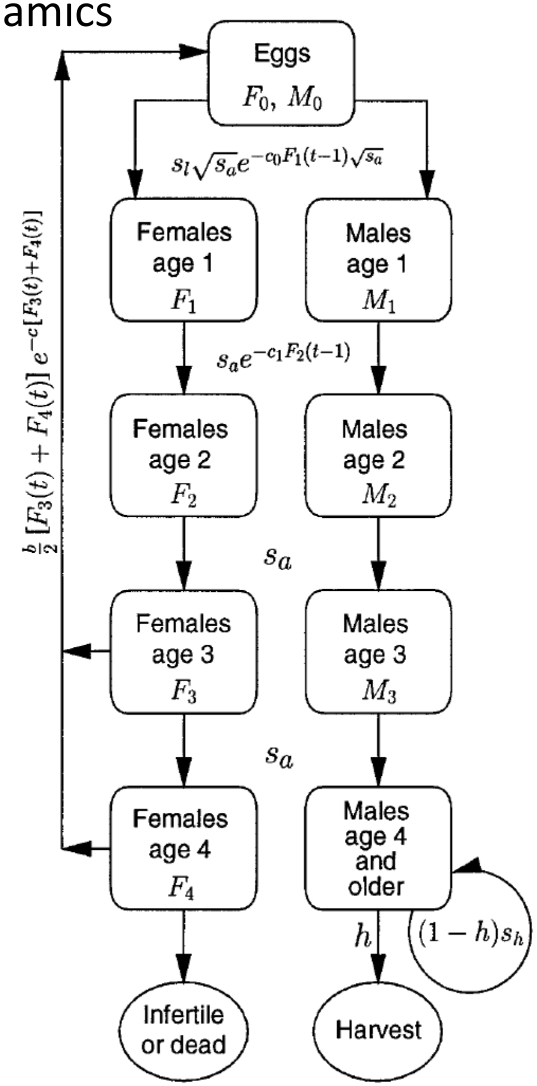
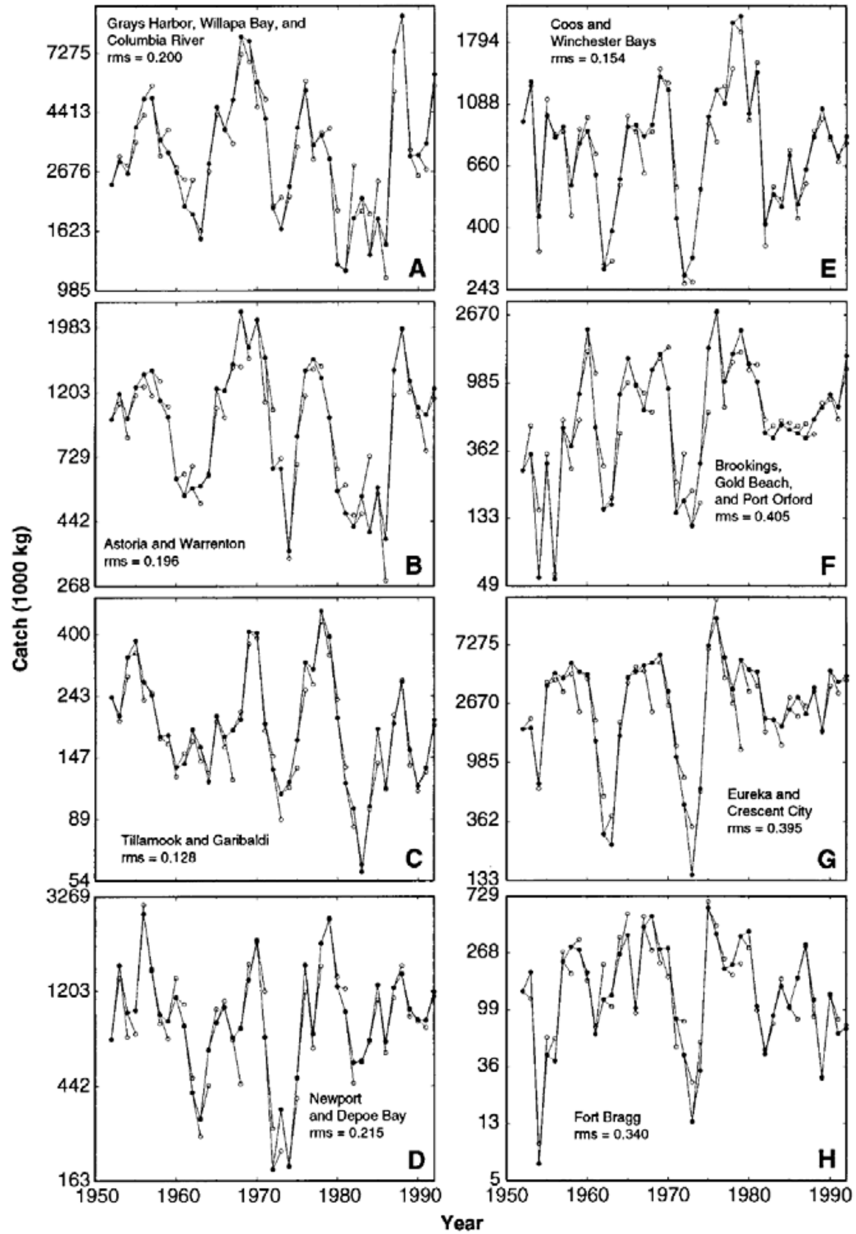
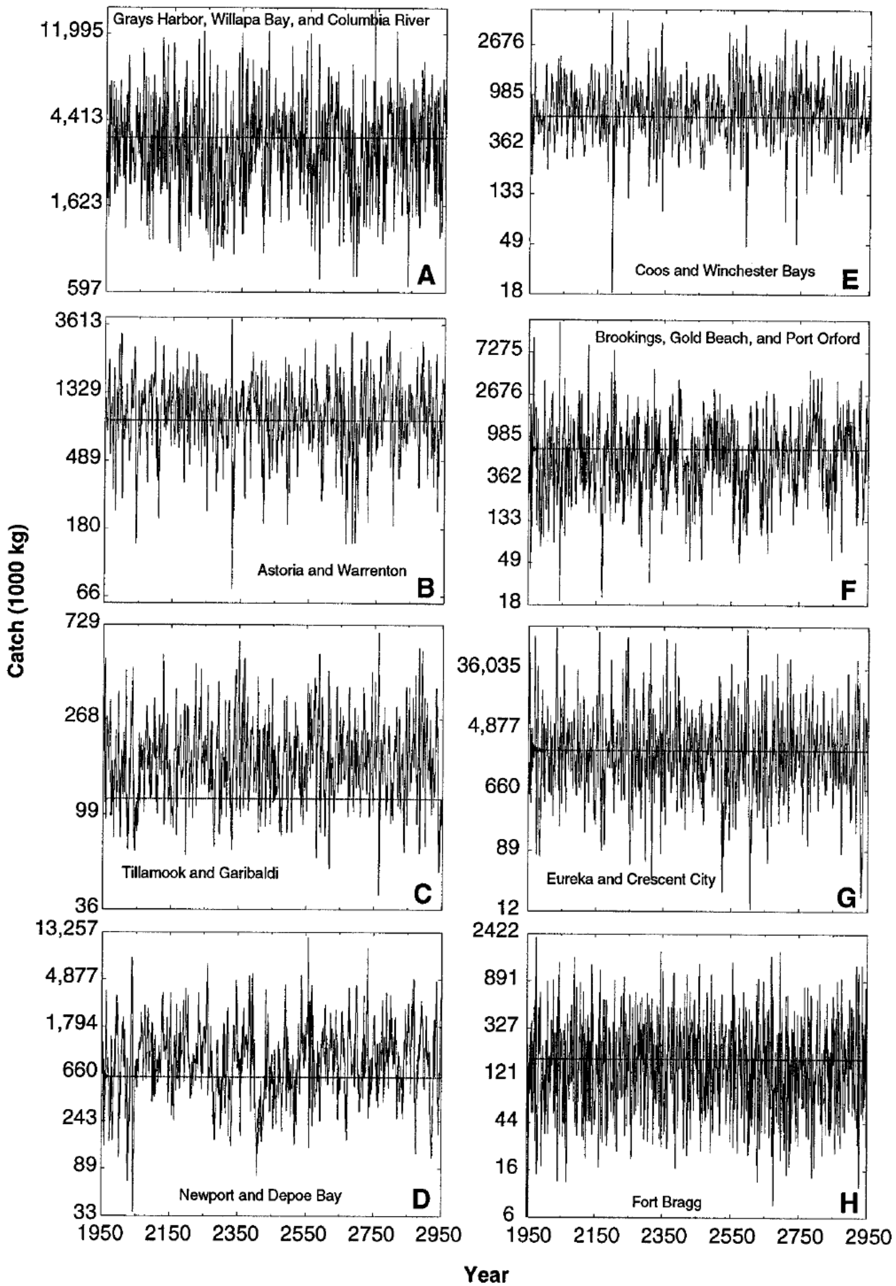


Observe this

Observed harvests and one step ahead predictions

Log scale of harvest





- Stochastic simulations over 1000 years; in all cases but one best fit parameters produce a stable equilibrium for deterministic skeleton
- Is right way to think of this as transients in response to stochastic perturbations?

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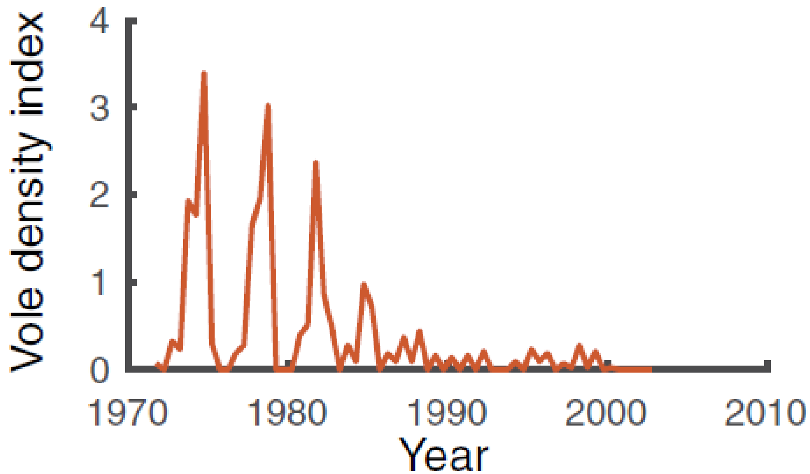

Population
abundance of voles in
northern Sweden,
showing a transition
from
large-amplitude periodic
oscillations to nearly
steady-state dynamics

B. Hörnfeldt, Long-term
decline in numbers of
cyclic voles in
boreal Sweden: Analysis
and presentation of
hypotheses. Oikos
107, 376–392 (2004).

Table 2. Empirical evidence for long ecological transients.

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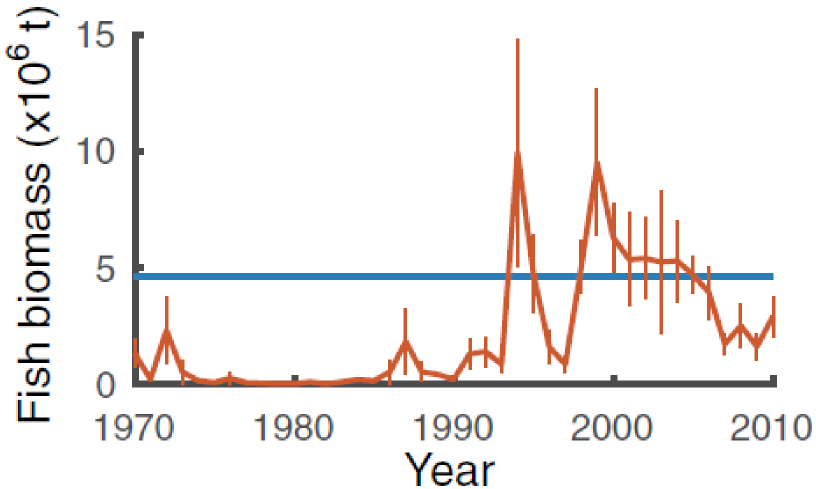

Biomass of forage fishes in the eastern Scotian Shelf ecosystem; a low-density steady state changes to a dynamical regime with a much higher average density [blue line is the estimated carrying capacity; error bars are SEM]

K. T. Frank, B. Petrie, J. A. Fisher, W. C. Leggett, Transient dynamics of an altered large marine ecosystem. Nature 477, 86–89 (2011).

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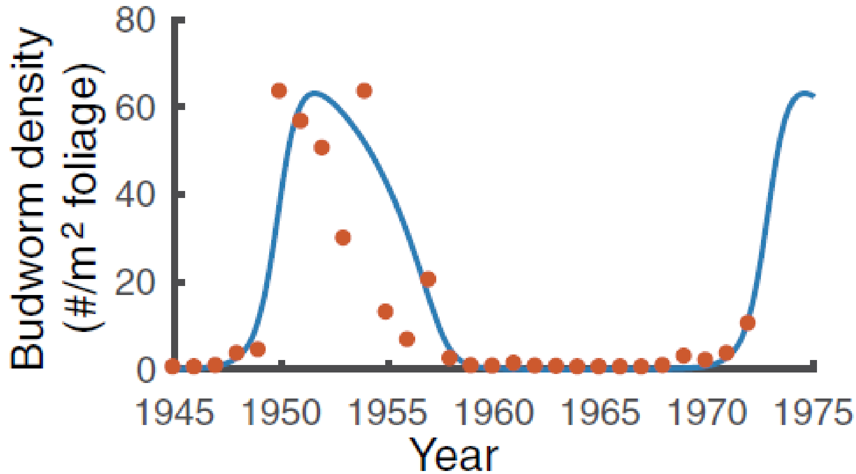
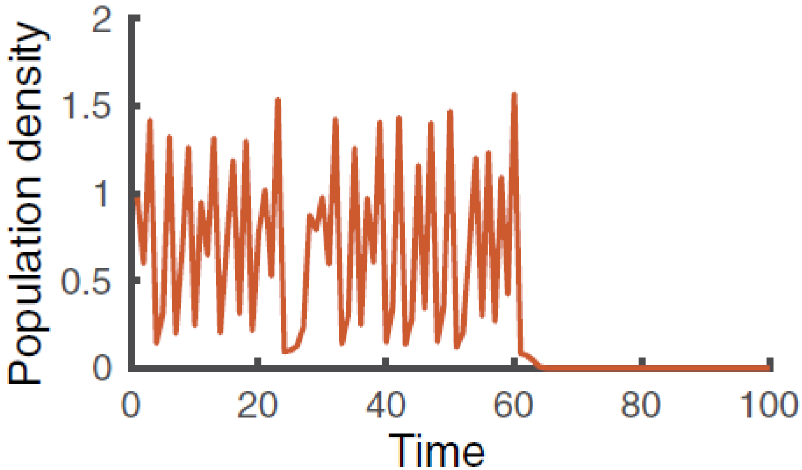


Spruce budworm [dots] has a much faster generation time than its host tree, resulting in extended periods of low budworm density interrupted by outbreaks.

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).

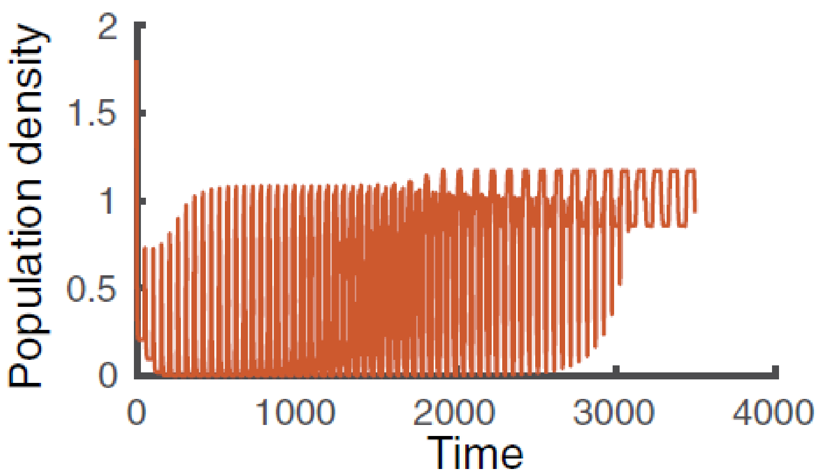
Simple models can show transitions in the absence of external changes



Model showing apparently sustainable chaotic oscillation suddenly results in species extinction.

S. J. Schreiber, Allee effects, extinctions, and chaotic transients in simple population models. Theor. Popul. Biol. 64, 201–209 (2003).

Simple models can show transitions in the absence of external changes



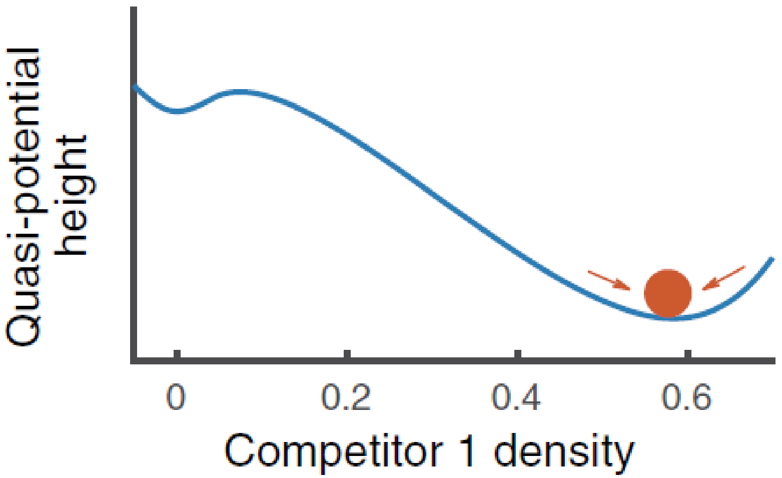
Model showing large-amplitude periodic oscillations that persist over hundreds of generations suddenly transition to oscillations with a much smaller amplitude and a verydifferent mean

A. Y. Morozov, M. Banerjee, S. V. Petrovskii, Long-term transients and complex dynamics of a stage-structured population with time delay and the Allee effect. J. Theor. Biol.
396, 116–124 (2016).

Dynamical systems ideas can help to ‘classify’ transients

- Ghost attractor

Illustration of ghost attractor in 2 species competition model



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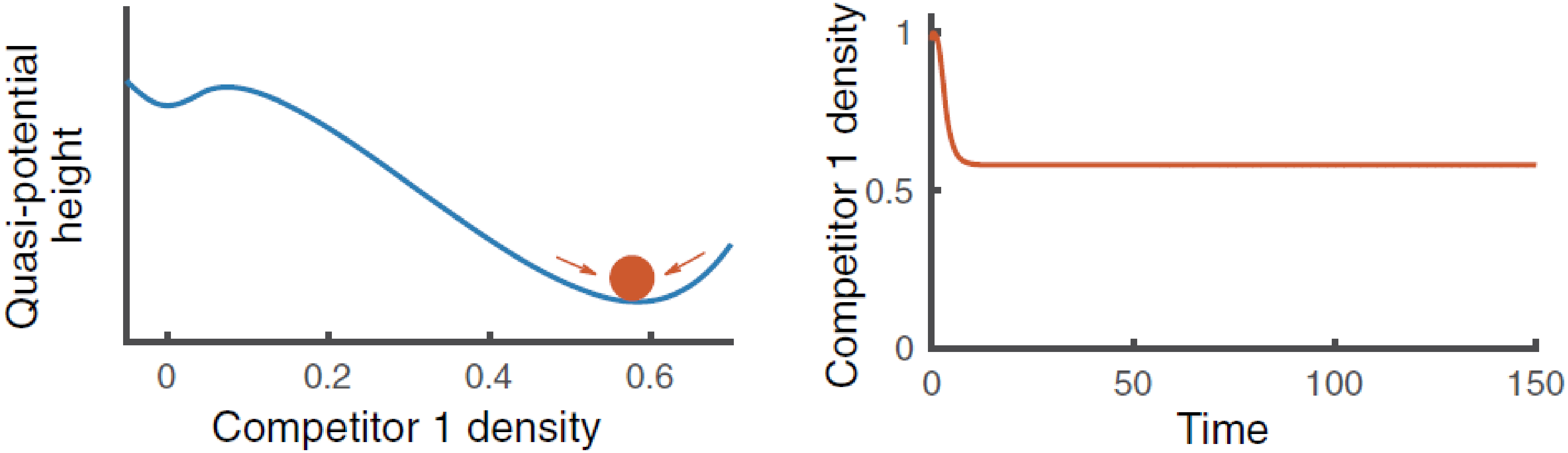

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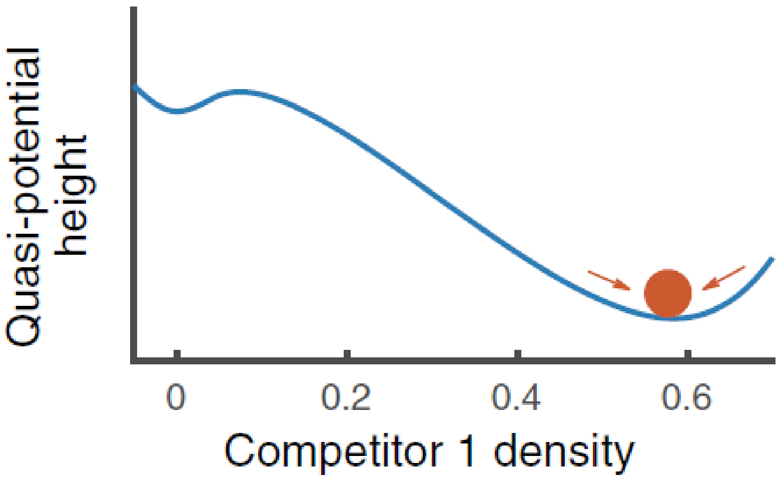

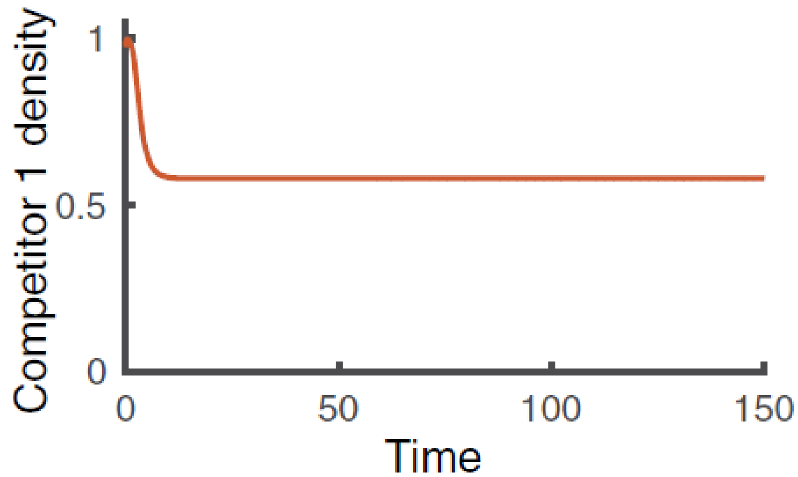

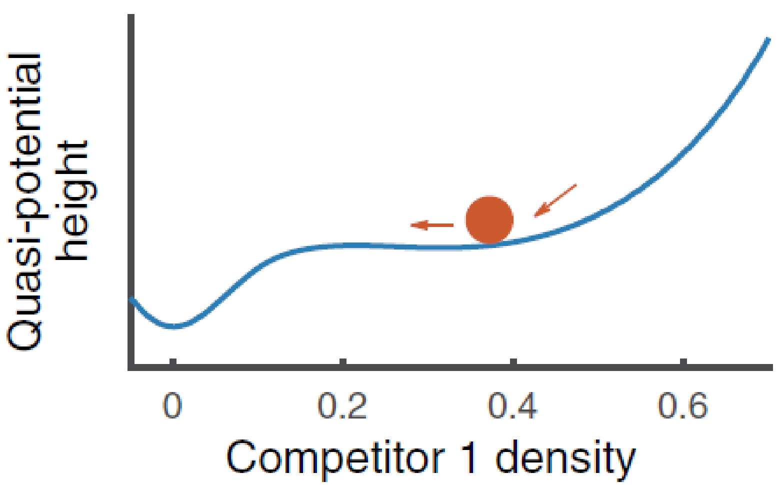

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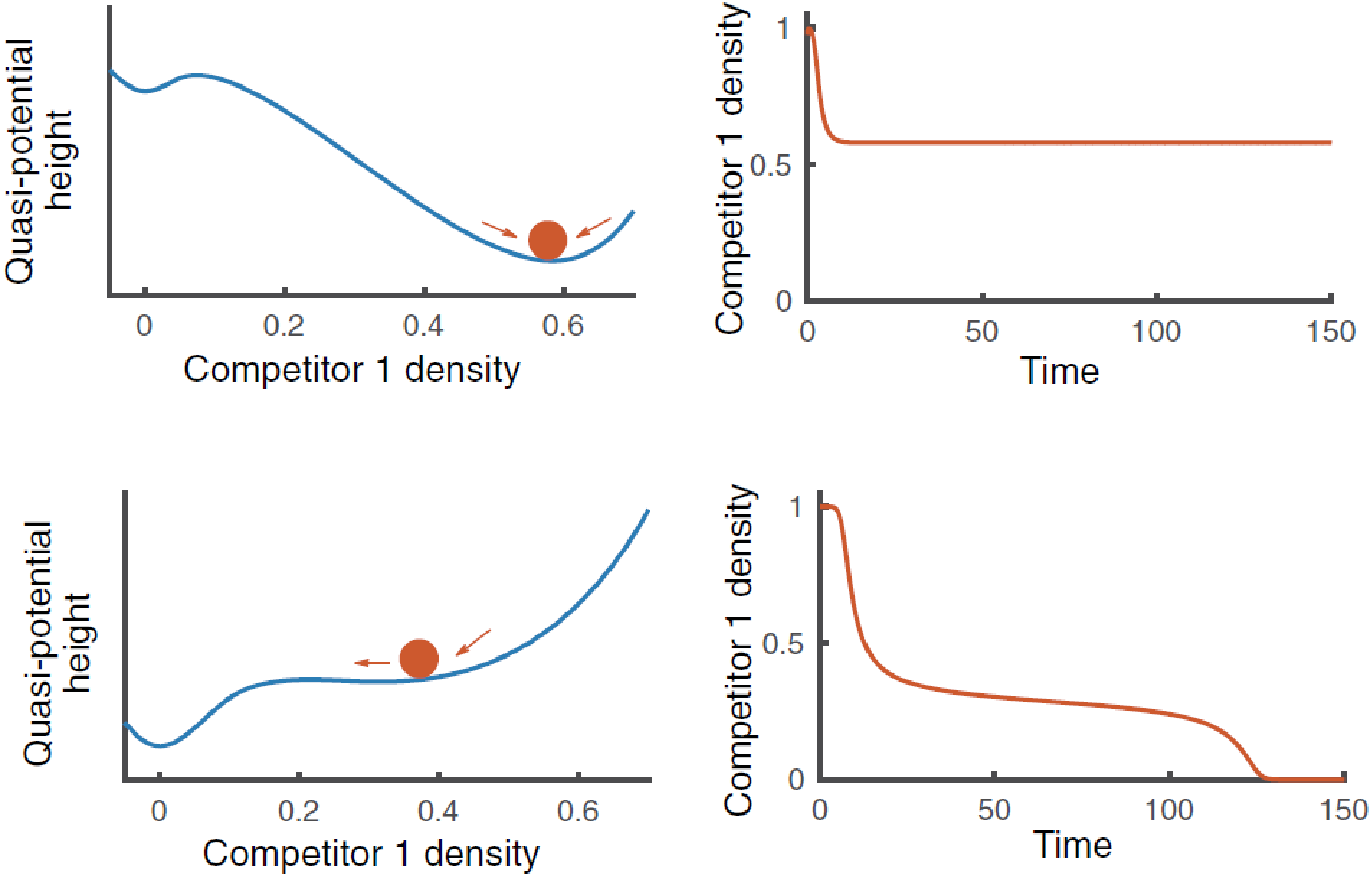

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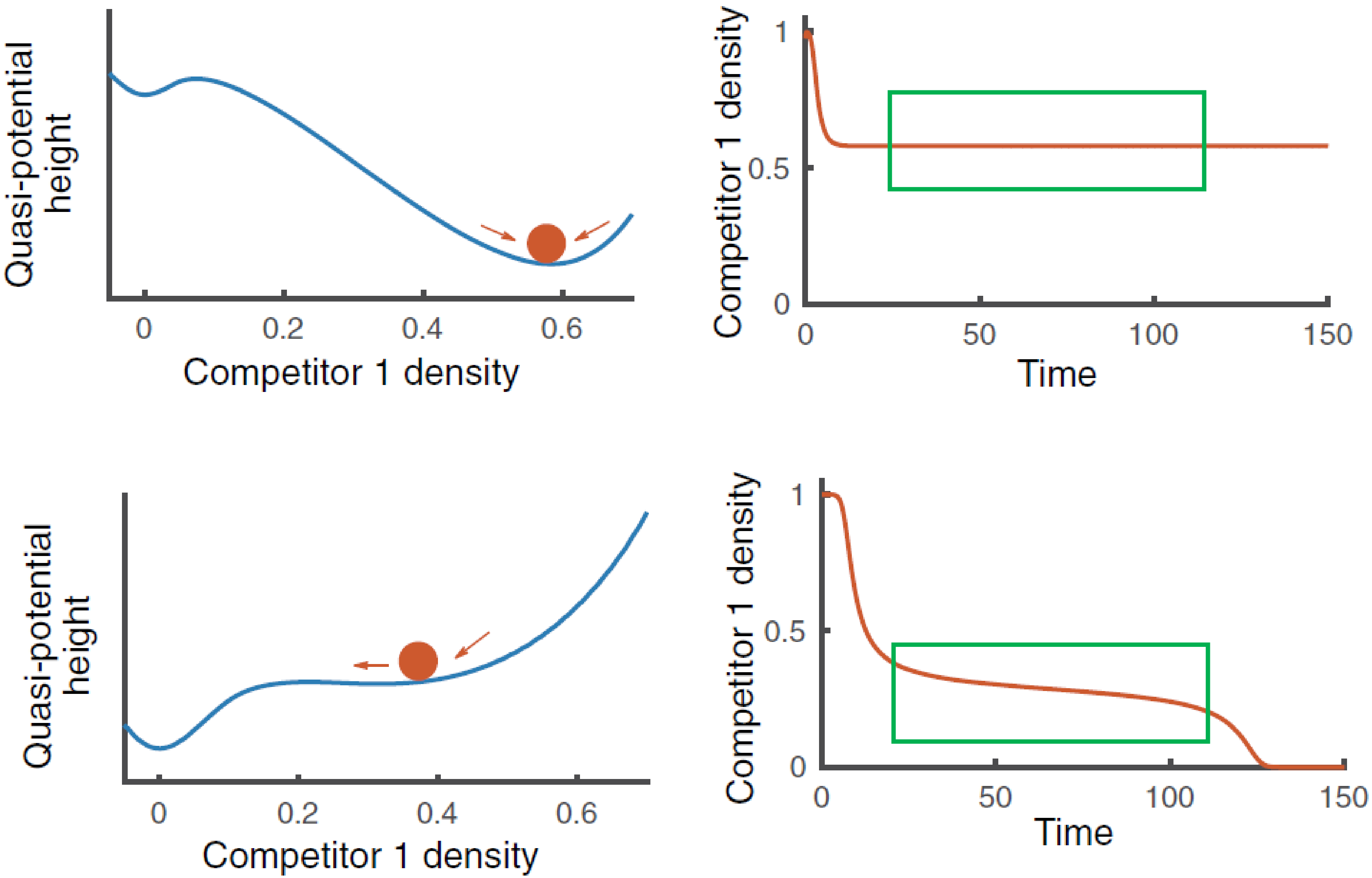
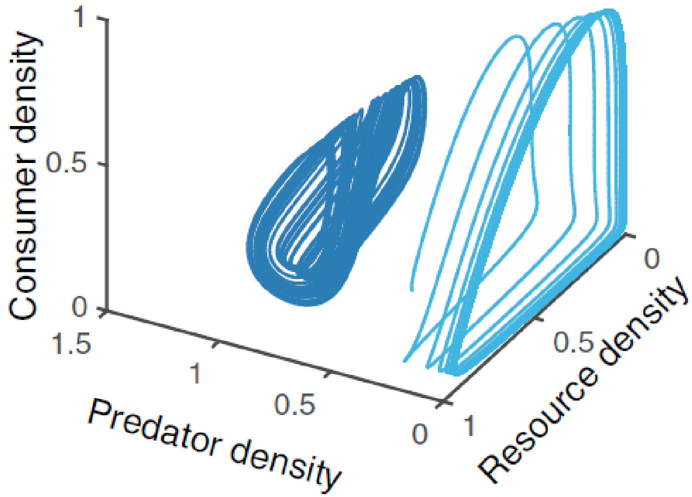


Illustration of ghost attractor in 3 species food chain



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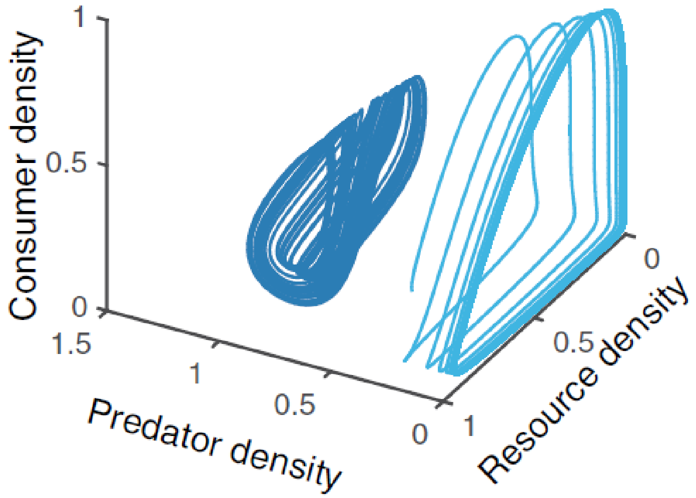

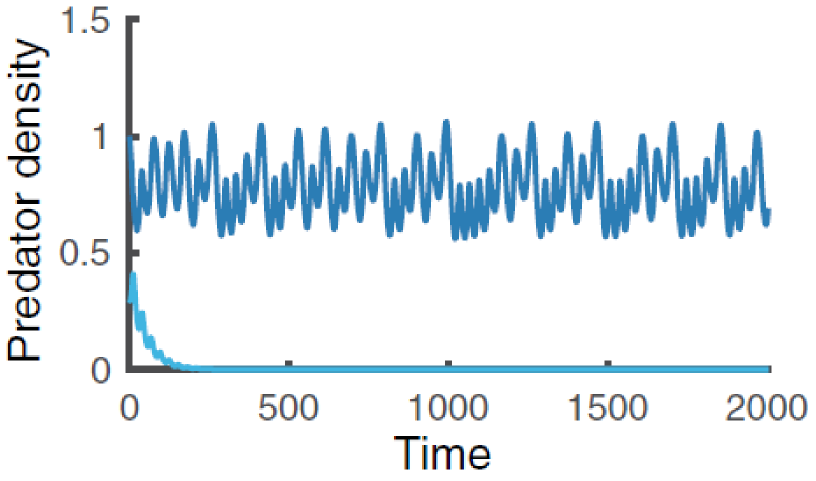

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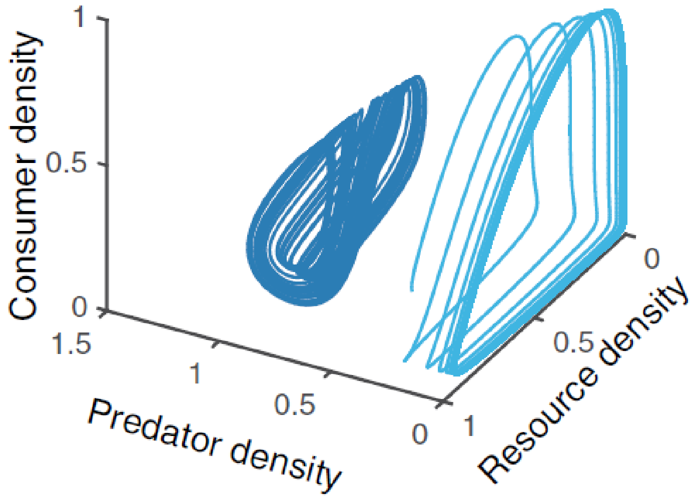

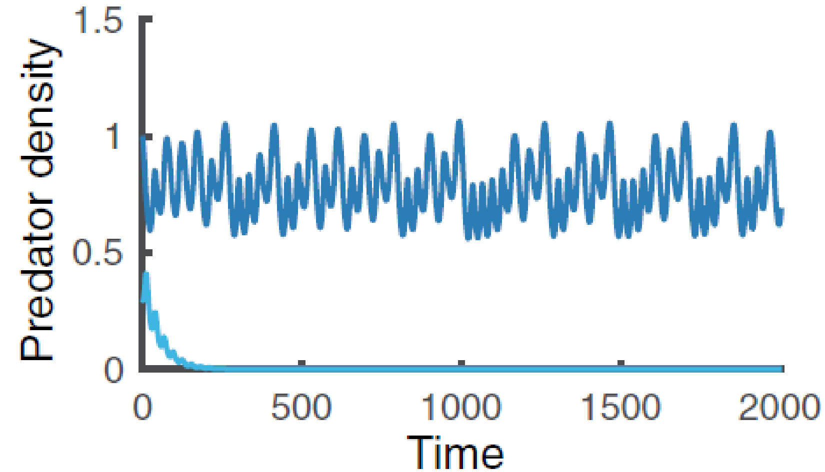

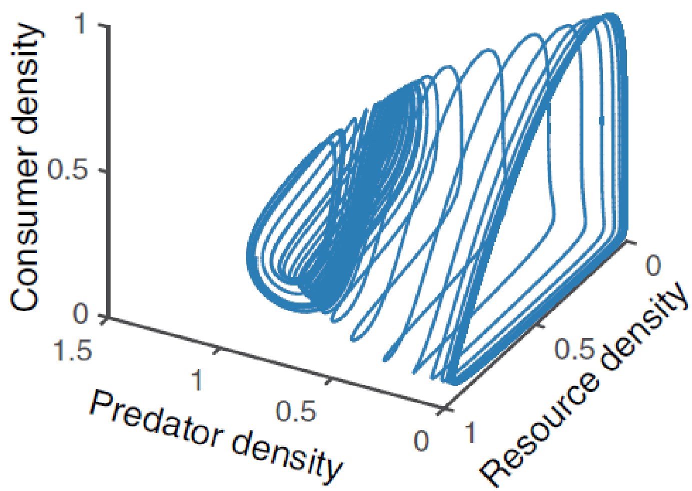

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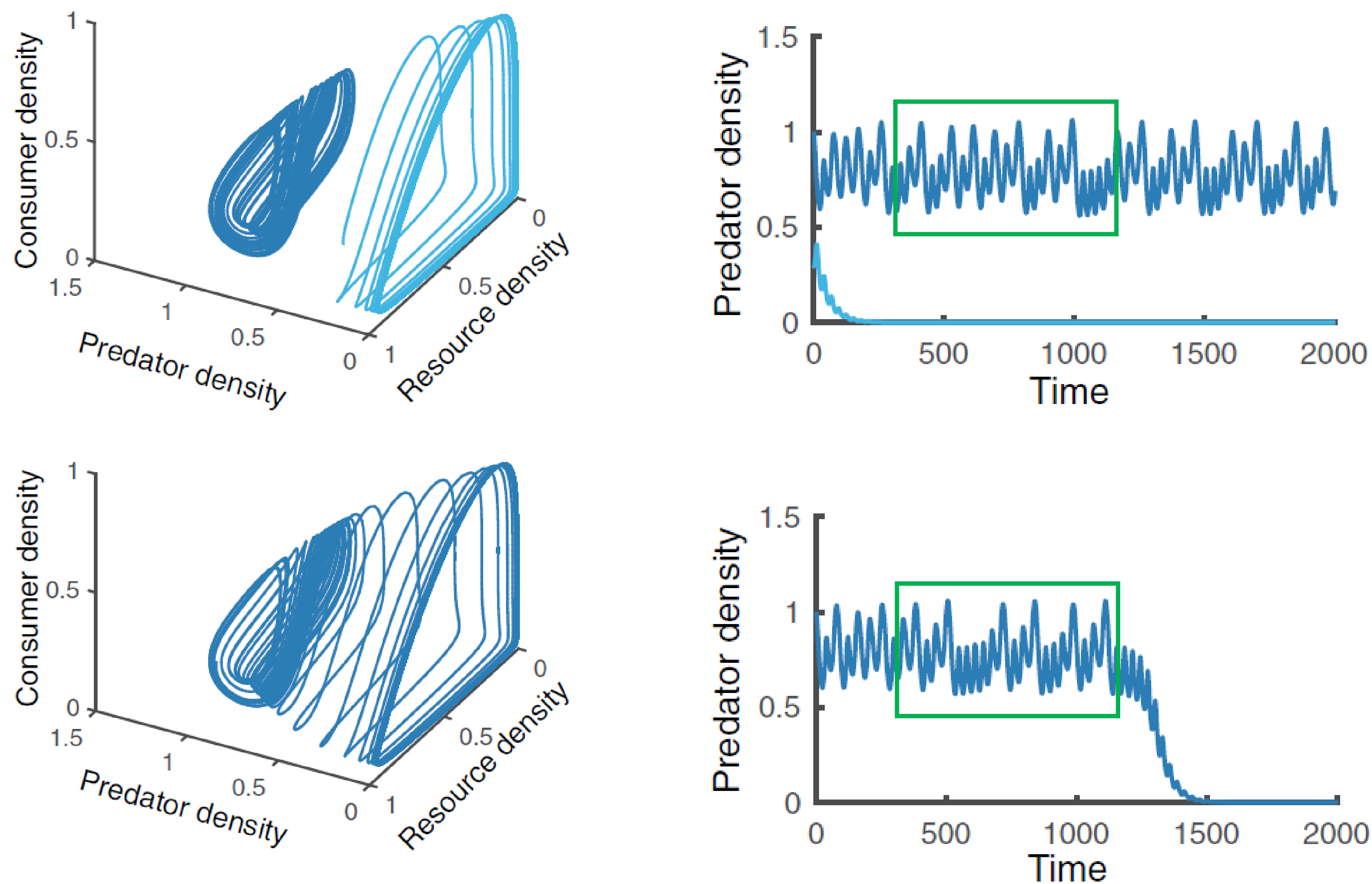
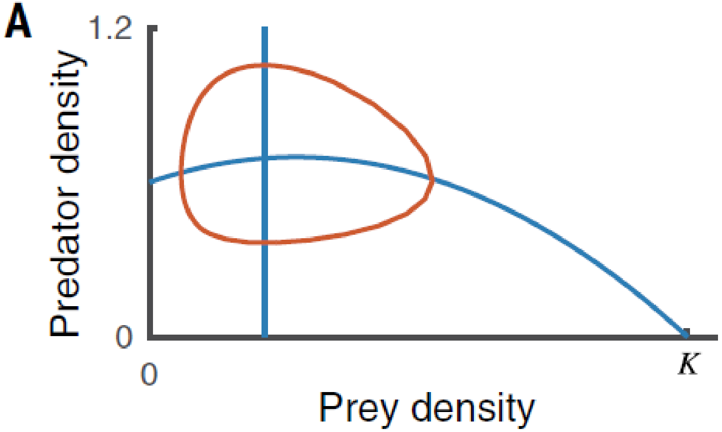


Dynamical systems ideas can help to ‘classify’ transients

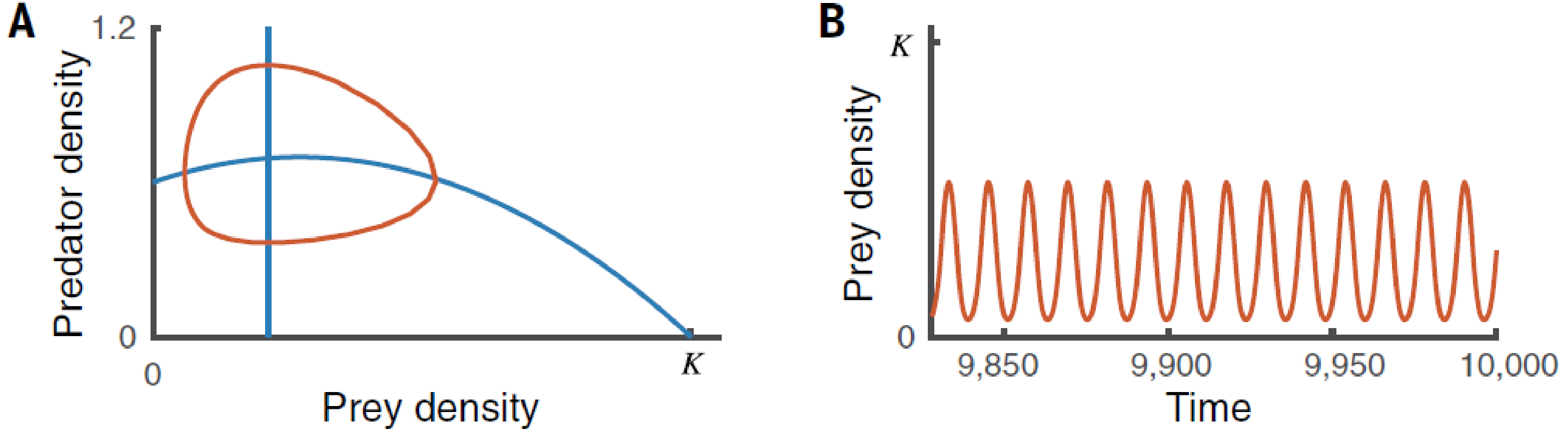
- Ghost attractor
- Crawl-bys

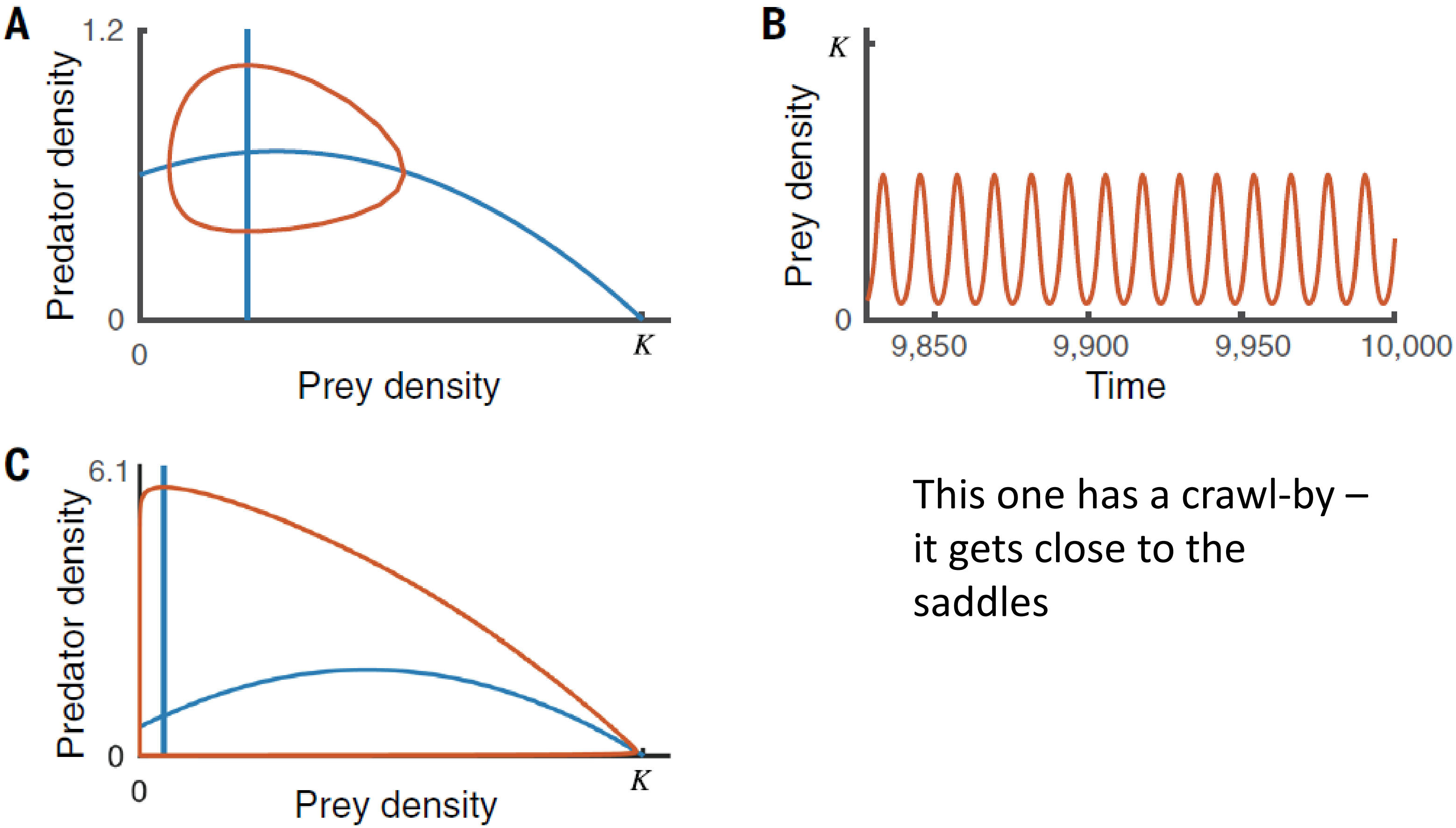
Predator-Prey dynamics

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

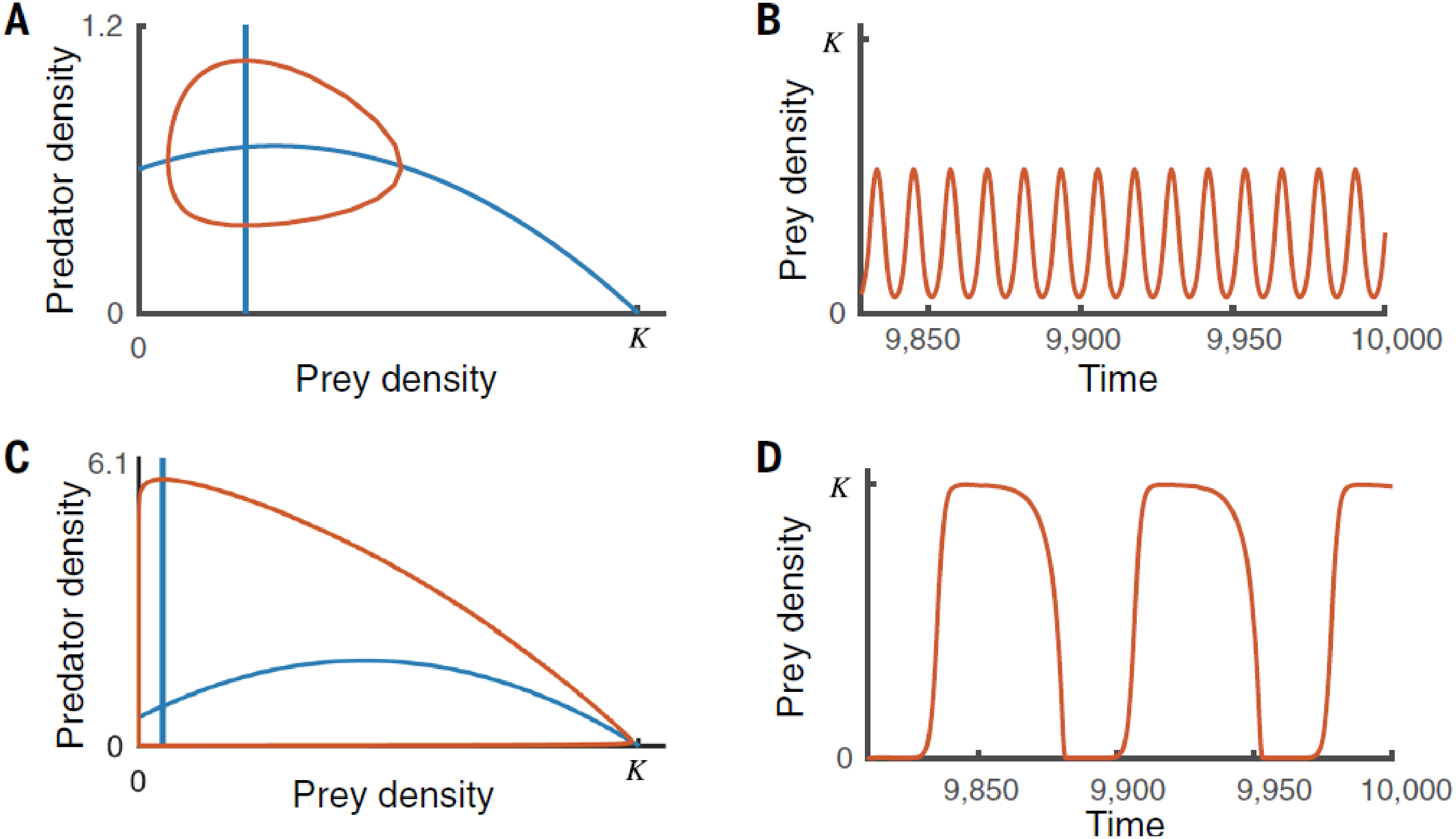


No transients for this predator prey dynamic as illustrated in a phase plane


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

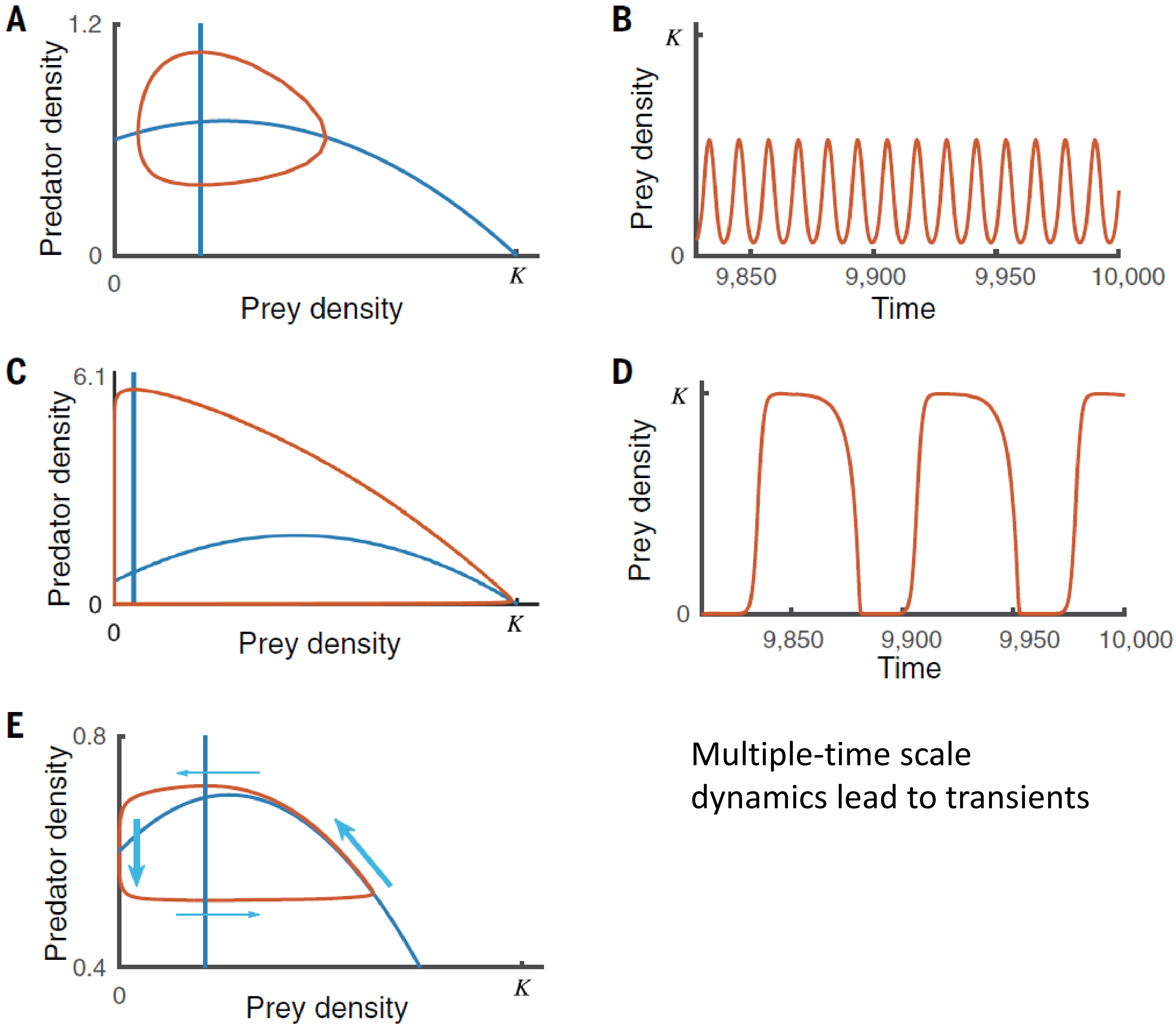


This one has a crawl-by – it gets close to the saddles

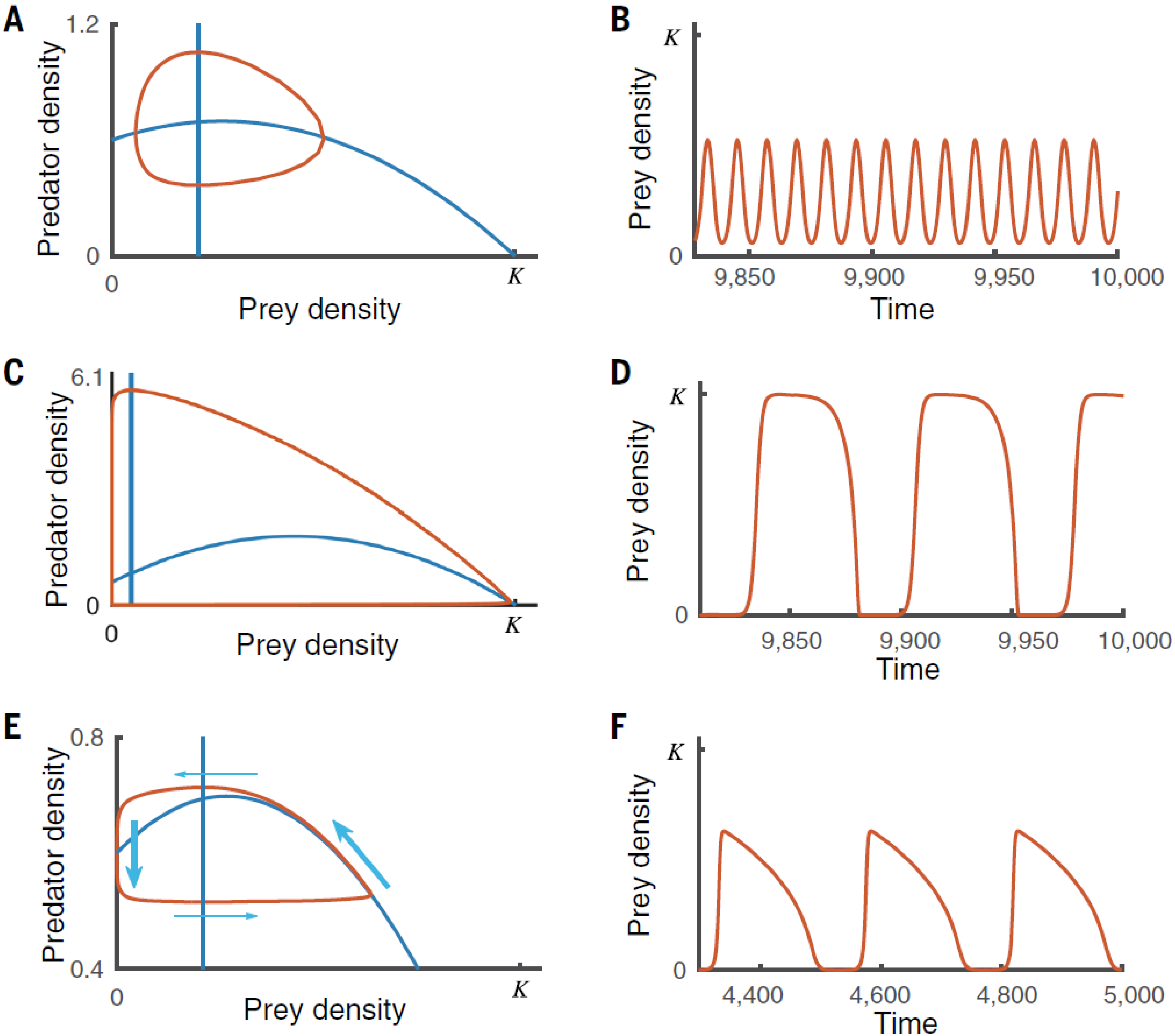

A
1.2
Predator density
0
0
K
Prey density
B
K
Prey density
0
9,850
9,900
9,950
10,000
Time
C
6.1
Predator density
0
0
K
Prey density
D
K
Prey density
0
9,850
9,900
9,950
10,000
Time

Dynamical systems ideas can help to ‘classify’ transients

- Ghost attractor
- Crawl-bys
- Slow-fast dynamics



Multiple-time scale
dynamics lead to transients



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

We have already seen high dimension and stochasticity

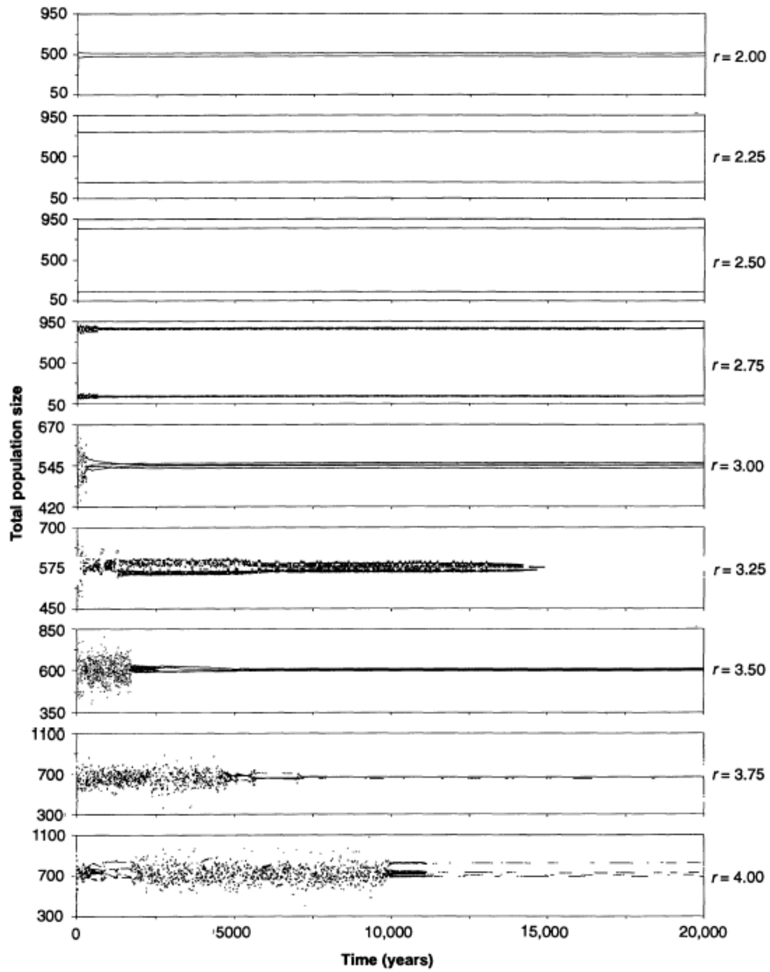
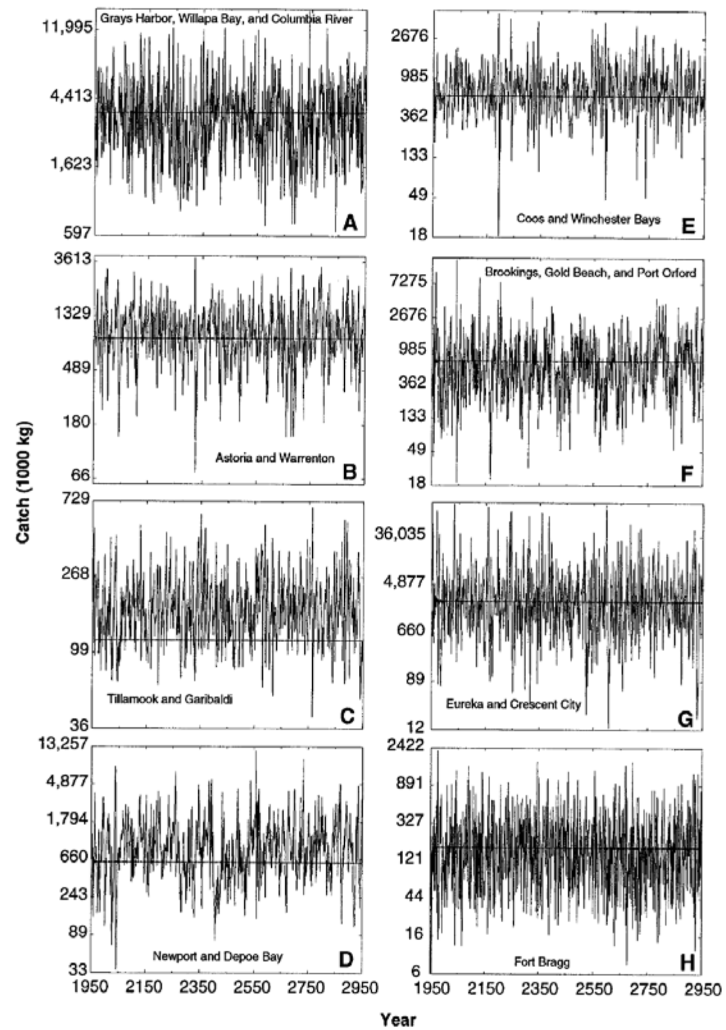


Fig. 1. Dynamics of a spatially structured model (*1–3*) of a population with pelagic larvae along a coastline as a function of the growth rate *r*. In all cases, the initial conditions were chosen randomly in space from a uniform distribution, and $D = 800$. The presence of long transients is apparent from the plots for all values of $r \geq 3.25$.



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		

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Cannot overemphasize how important this is for management

Ecosystems can have multiple stable states

Ecosystems can have multiple stable states

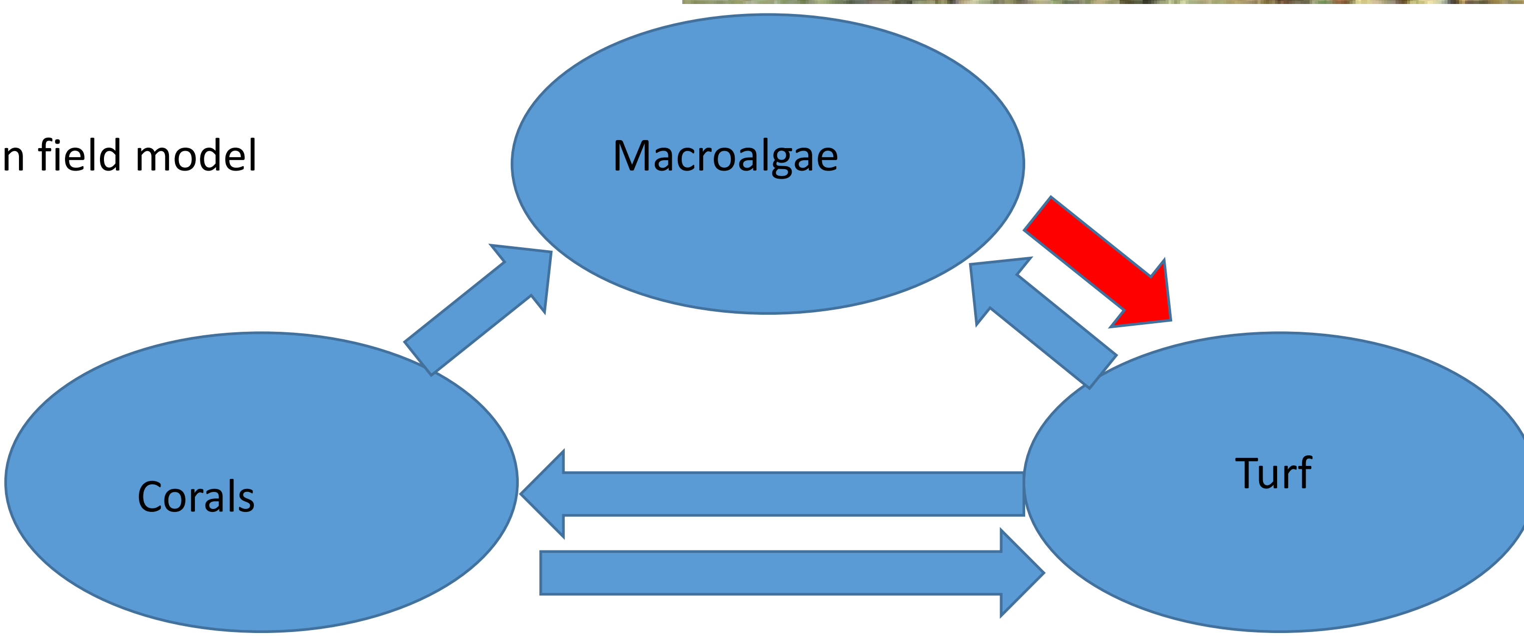
An example: coral reefs and grazing

- Demonstrate the role of hysteresis in coral reefs by extending an analytic model (Mumby *et al*. 2007*) to explicitly account for parrotfish dynamics (including mortality due to fishing)
- Identify when and how phase shifts to degraded macroalgal states can be prevented or reversed
  - Provide guidance to management decisions regarding fishing regulations
  - Provide ways to assign value to parrotfish

*Mumby, P.J., A. Hastings, and H. Edwards (2007). "Thresholds and the resilience of Caribbean coral reefs." *Nature* **450**: 98-101.

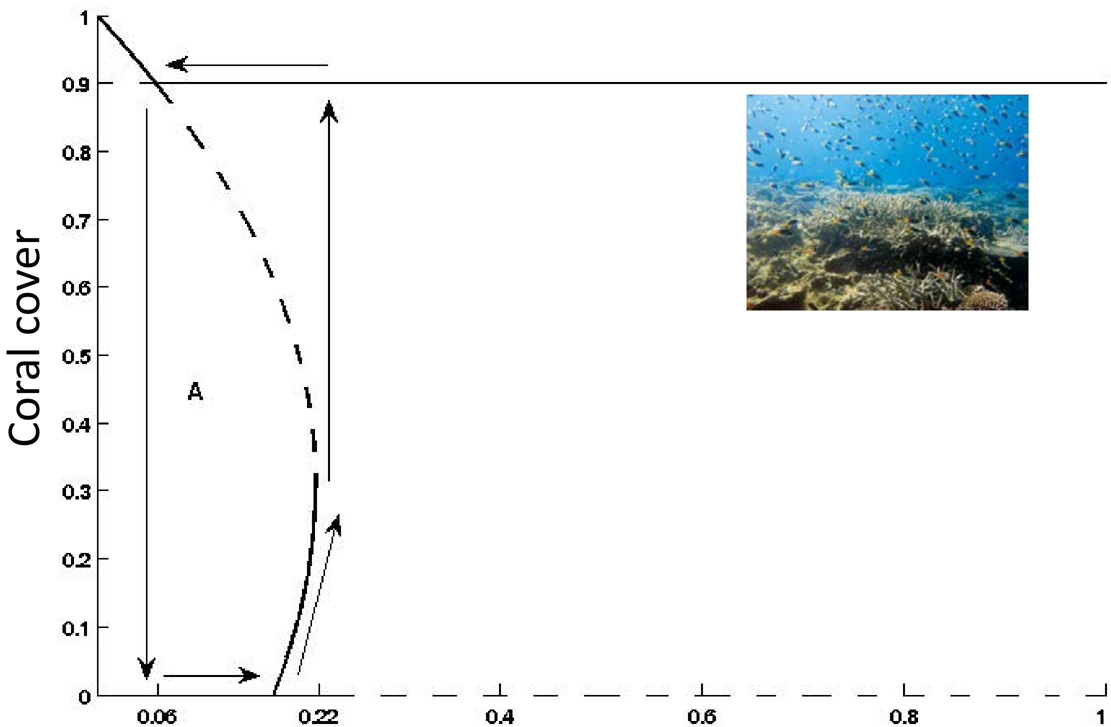
Grazing a key driver for corals

Use mean field model



Grazing

Outome depends on grazing intensity – hysterisis



Grazing intensity (will depend on fish population)

- Coral cover versus grazing intensity using the original model
- Solid lines are stable equilibria, dashed lines are unstable
- Arrows denote the hysteresis loop resulting from changes in grazing intensity
- The region labeled “A” is the set of all points that will end in macroalgal dominance without proper management

Simple analytic model

Overgrowth

$$\frac{dM}{dt} = \boxed{aMC} - \frac{g(P)M}{M+T} + \gamma MT$$

$$\frac{dC}{dt} = rTC - dC - \boxed{aMC}$$ Overgrowth

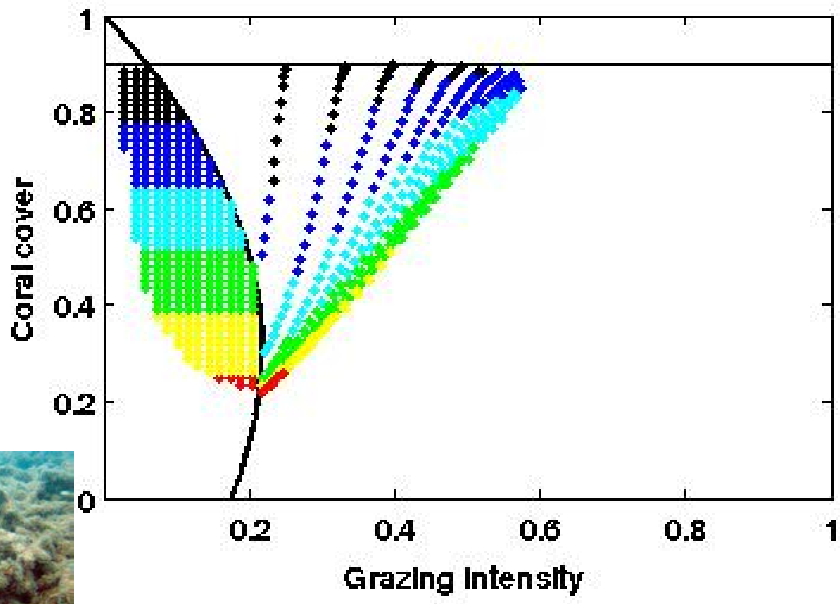
$$\frac{dP}{dt} = sP\left(1 - \frac{P}{K(C)}\right) - fP$$

- Blackwood, Hastings, Mumby, Ecol Appl 2011; Theor Ecol 2012

- But parrotfish are subject to fishing pressure, so need to include the effects of fishing and parrotfish dynamics, and only control is changing fishing

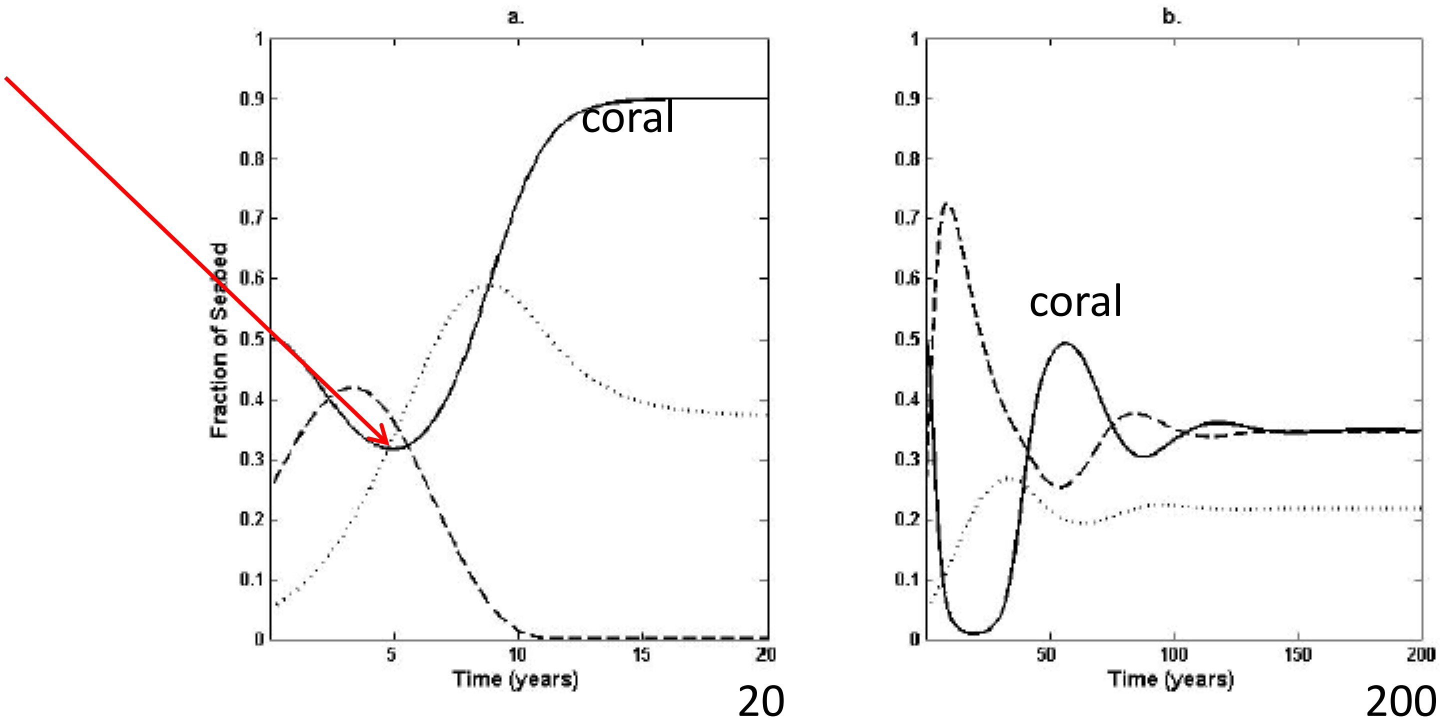
Coral recovery via the elimination of fishing effort

Start with macroalgae at long term equilibrium



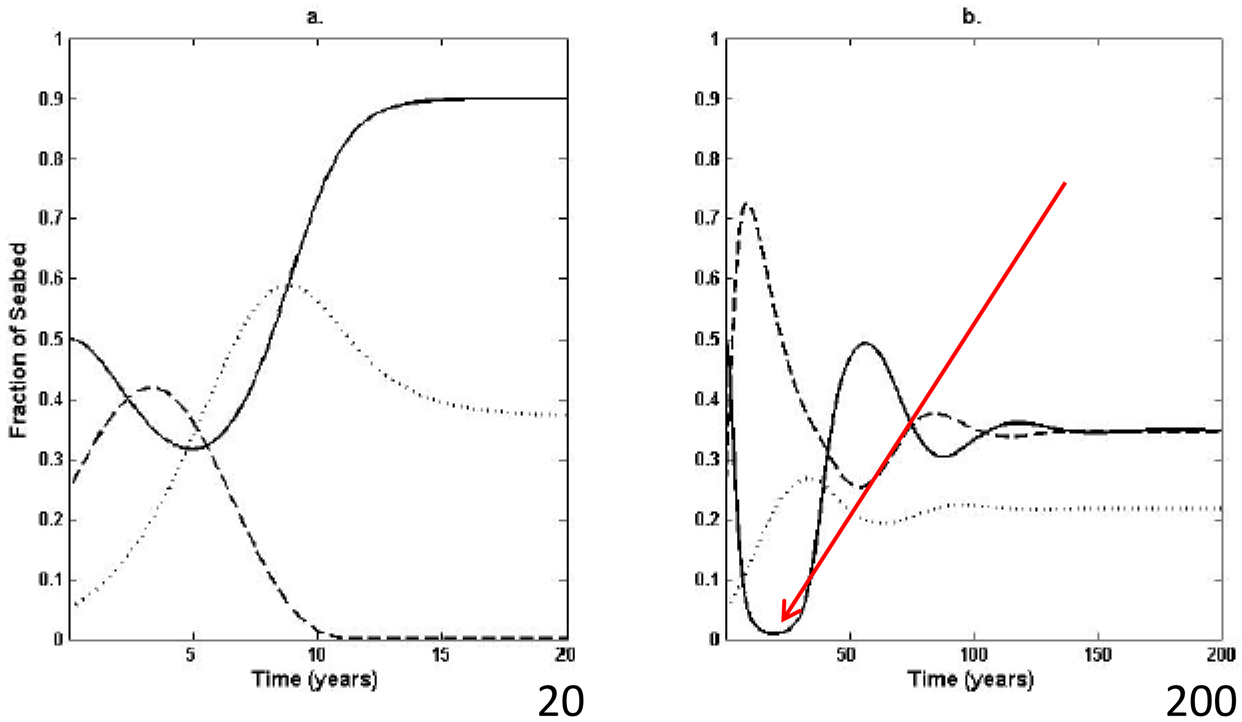
- Points in the colored region are points that can be controlled to a coral-dominated state and the points outside of the region are the ending location after 5 years with no fishing mortality

Recovery time scale depends on fishing effort level and is not monotonic



Complete reduction of fishing on the left

Recovery time scale depends on fishing effort level and is not monotonic



More realistic by 65% reduction of fishing on the right

Conclusions

- Transient dynamics are key for answering important ecological questions on relevant timescales
- Transient dynamics are important for management
- Many ecological systems definitely exhibit transient dynamics
- Distinguishing transient dynamics from asymptotic behavior is a challenge
- Concepts from dynamical systems provide a way to classify and understand transients (why and when)
- Further challenges from non-autonomous systems
- Tipping points are a phenomenon that is associated with transients

Mathematical challenges

- Dynamical systems with realistic stochasticity on realistic time scales and possible nonautonomous aspects