Alternative stable states, phase shifts, catastrophic transitions

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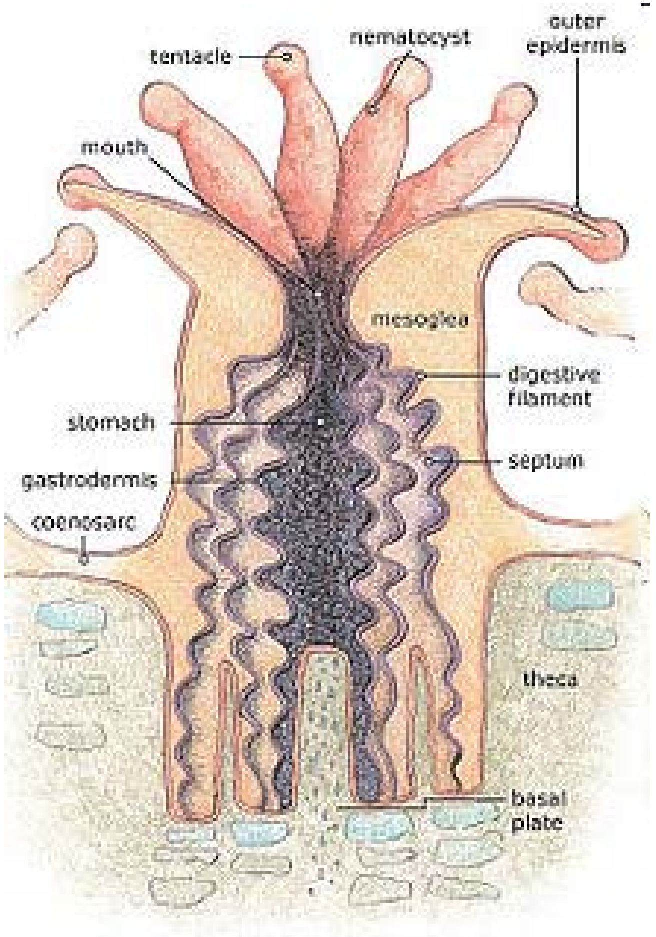
Outline

- Alternative stable states in coral reefs
- Phase shifts and alternative stable states
- Icelandic midges
- Bee decline
- Learning outcomes

Coral Reefs

- Coral reefs are made out of colonies of “polyps”. Reef building corals belong to the phylum Cnidaria
- Occur in nutrient poor waters
- They have tentacles to capture prey
- Polyps secrete calcium carbonate, that accumulate and forms the reef
- Reproduction mainly asexual through budding



Coral Reefs

- Coral reefs are highly diverse both in terms of corals as in other marine animals




Coral Reefs

- Corals compete for space with algae and macroalgae
- If space opens up all players will try to fill it
- Algae and macroalgae can overgrow a coral, coral can invade algal turfs

Blue tangs swimming in an elkhorn coral forest

Coral overgrown with macroalgae

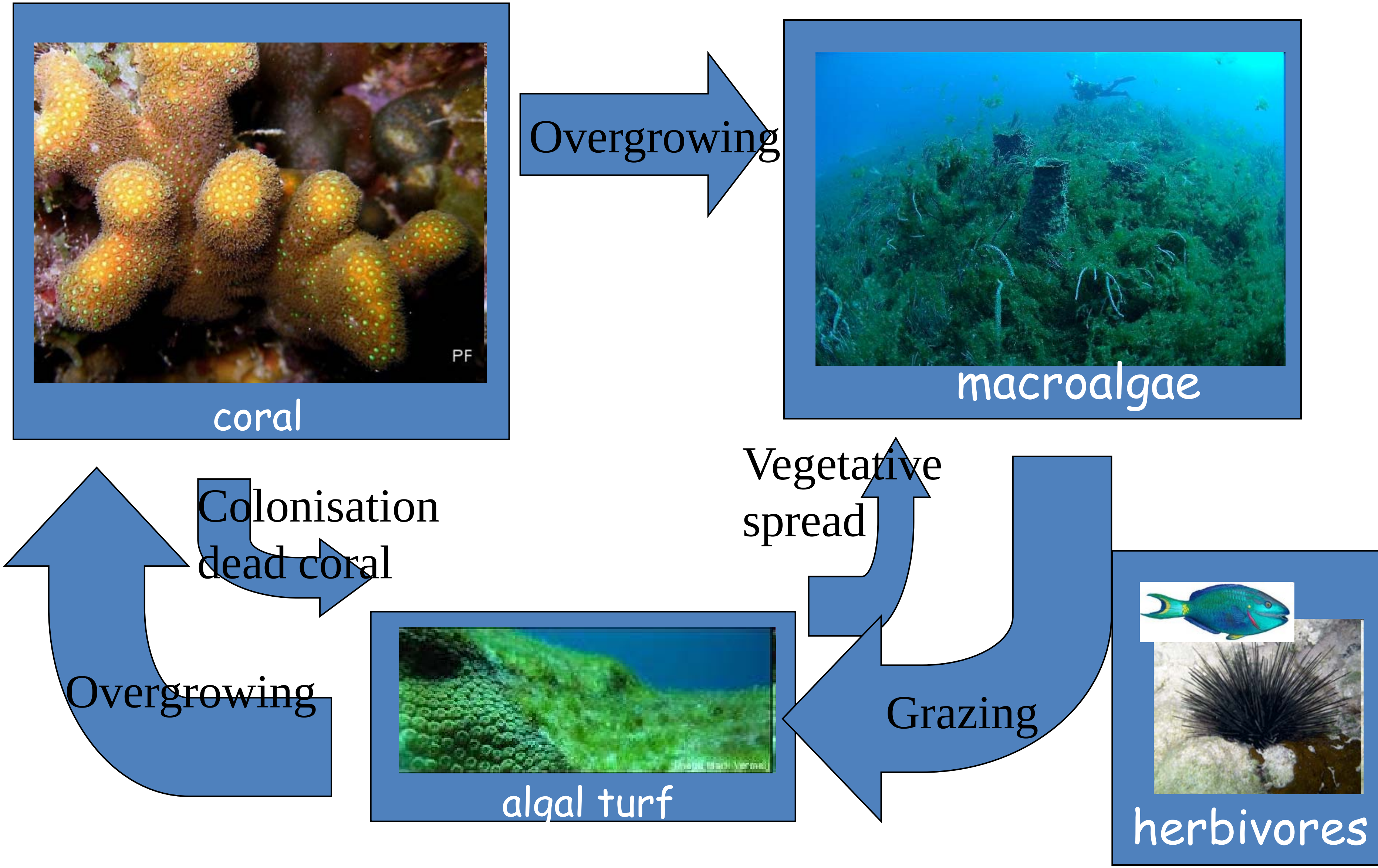
Coral reefs

Even though algae can overgrow coral, this normally is prevented through herbivores, who feed on the macroalgae

Diadema antillarum
(long spined sea urchin)

Parrot fish

Simplified Coral Reef Ecology



The same information, put in a model

$$\frac{\mathrm{d}M}{\mathrm{d}t} = aMC - \frac{gM}{M+T} + \gamma MT$$

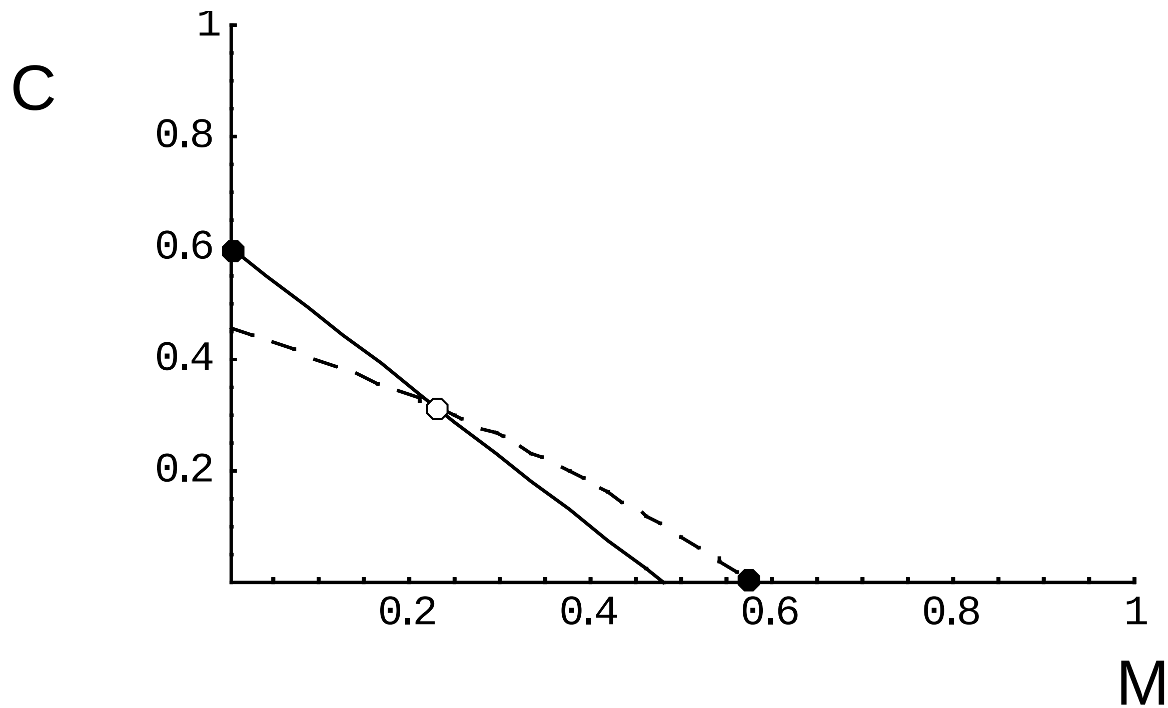
$$\frac{\mathrm{d}C}{\mathrm{d}t} = rTC - dC - aMC$$

with $T+M+C=1$

M, C and T describe the amount of space covered by Macroalgae, algal Turf and Coral

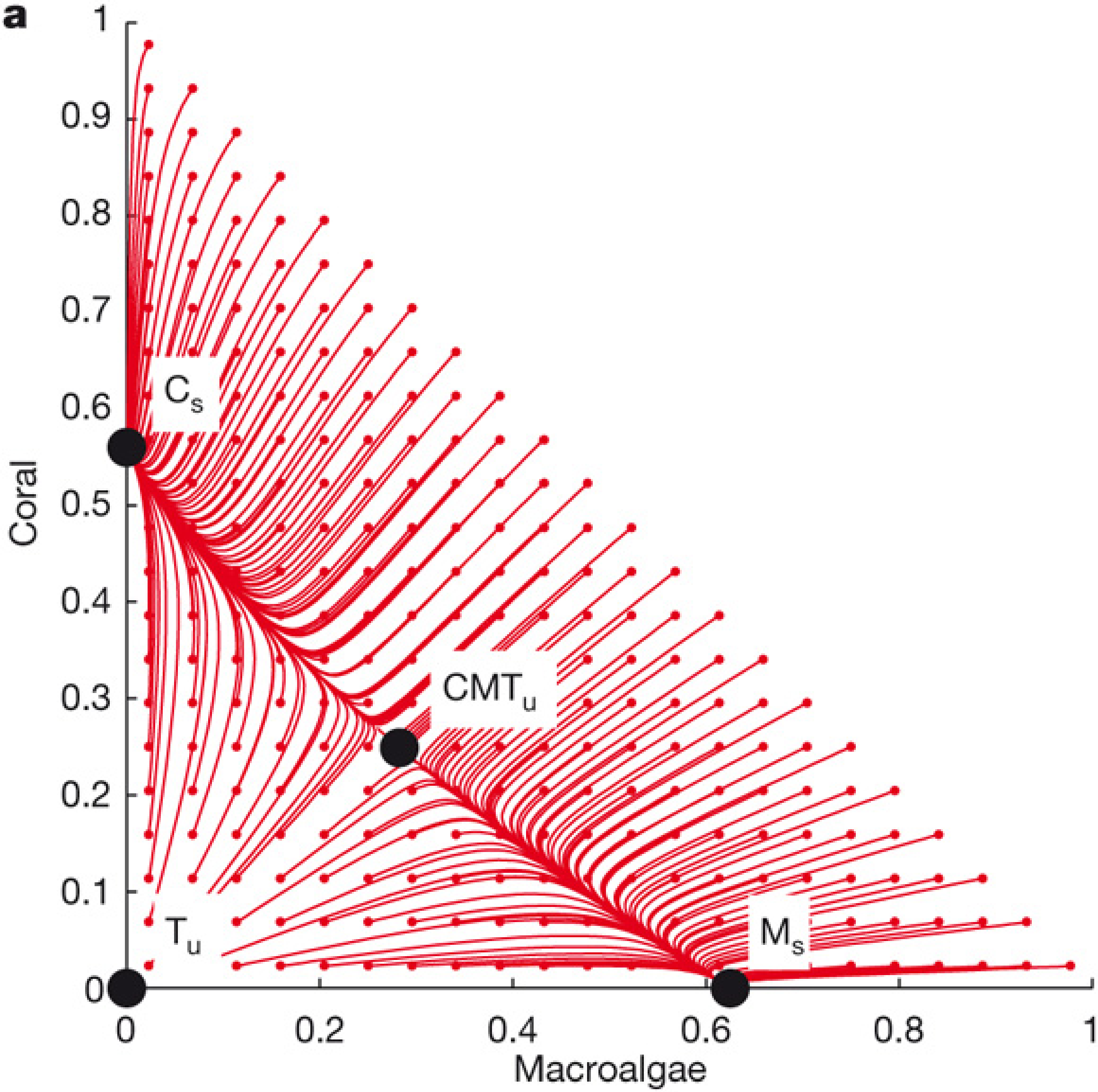
From: Mumby et al. Nature (2007)

Isoclines for the coral reef model

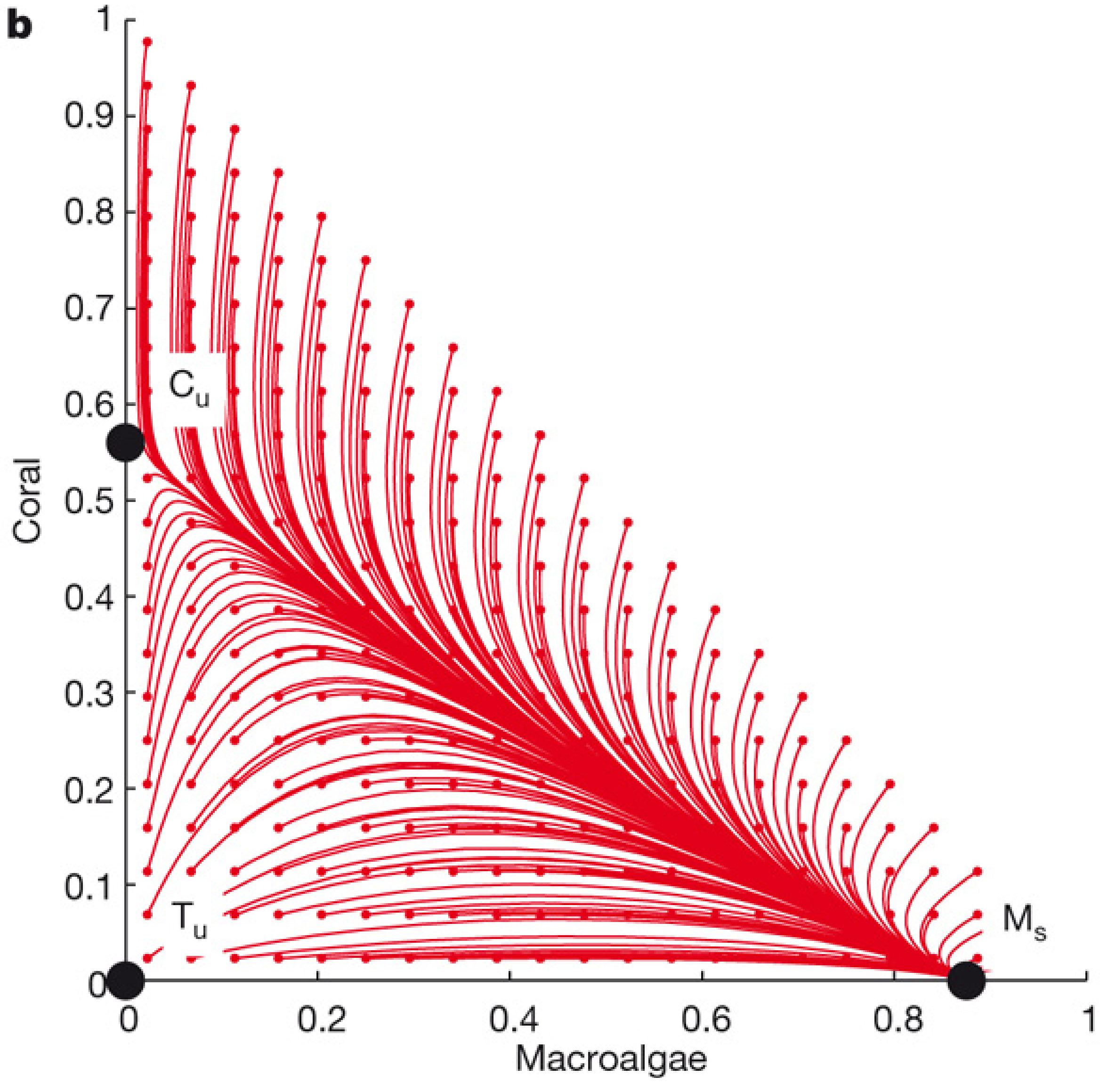


In the model, changing the amount of grazing, which determines the death rate of the macroalgae, is much the same as reducing the carrying capacity of the macroalgae.

a

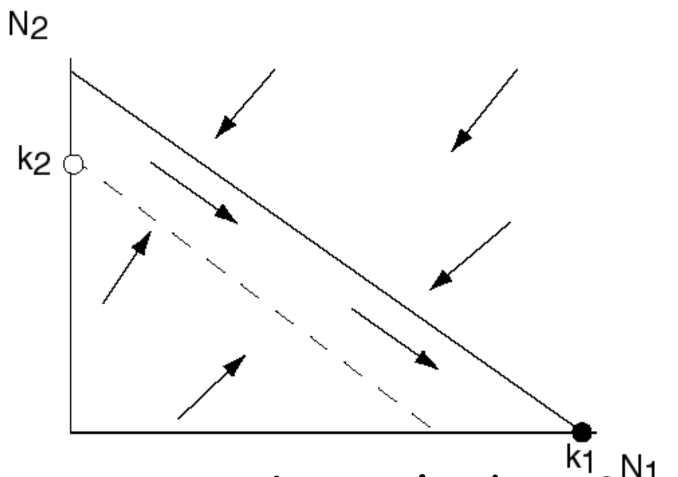


Coral
Macroalgae
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
0.2
0.4
0.6
0.8
C_s
CMT_u
T_u
M_s

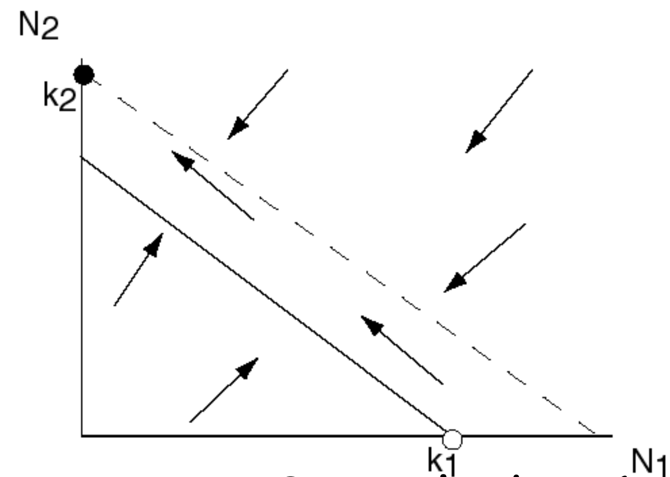


b
Coral
Macroalgae
C
u
T
u
M
s
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
0
0.2
0.4
0.6
0.8
1

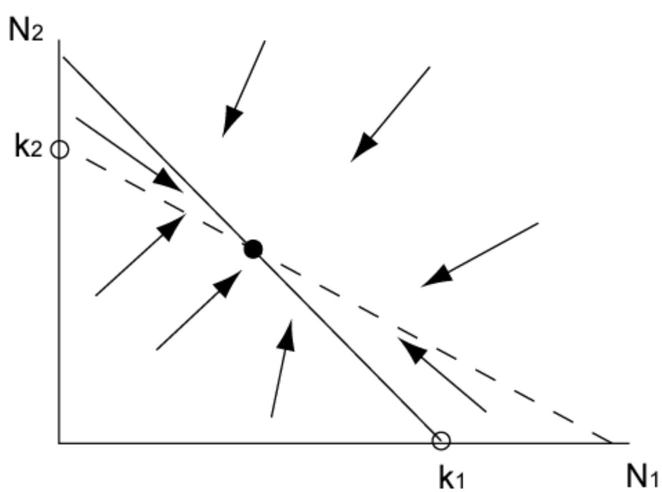
The outcomes of competition



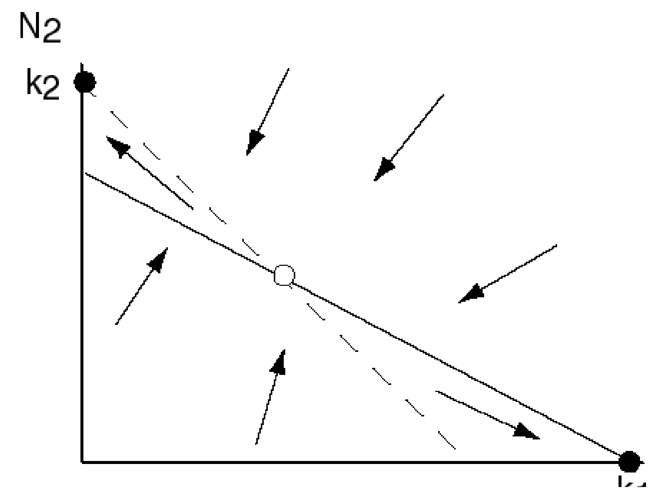
Species 1 excludes 2



Species 2 excludes 1

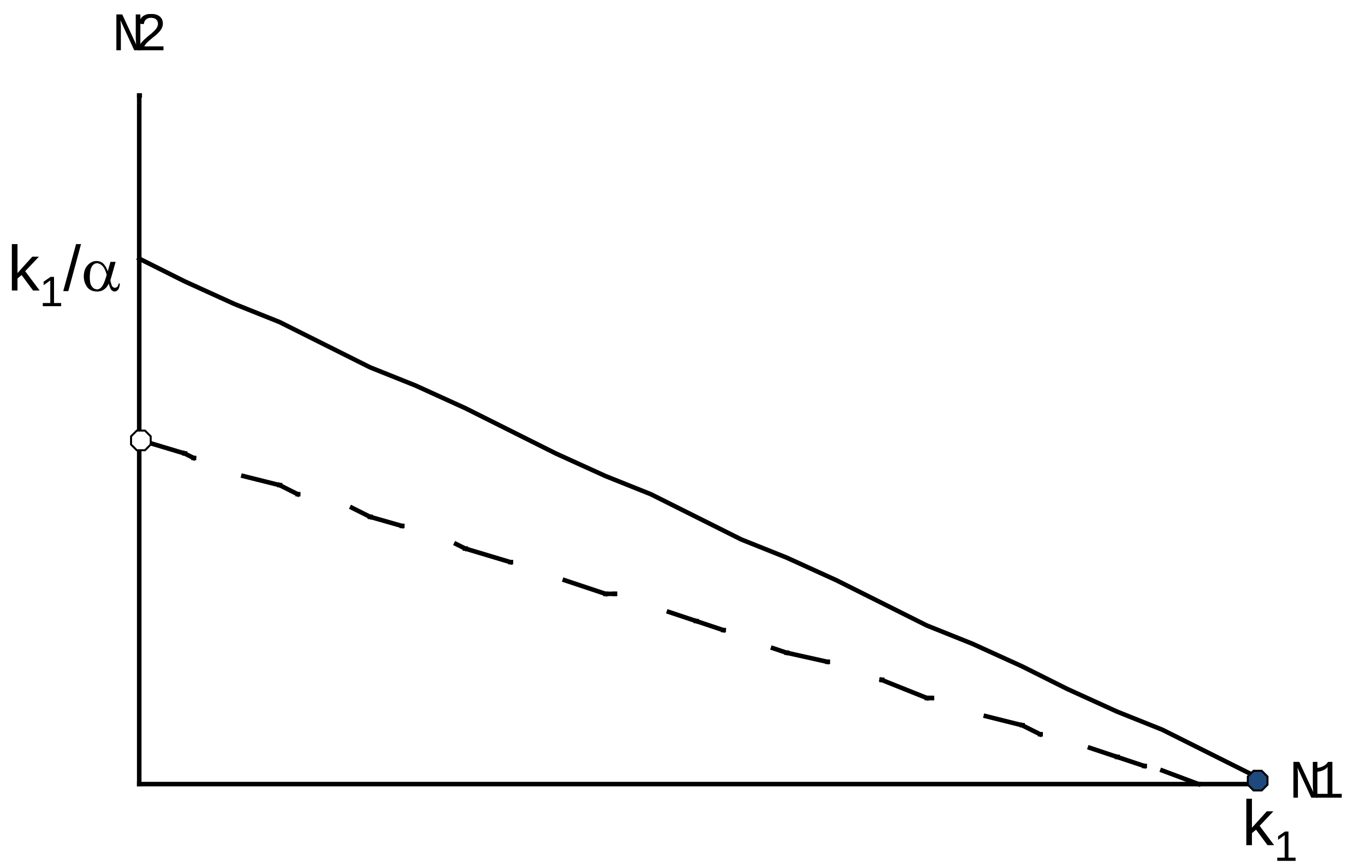


Coexistence

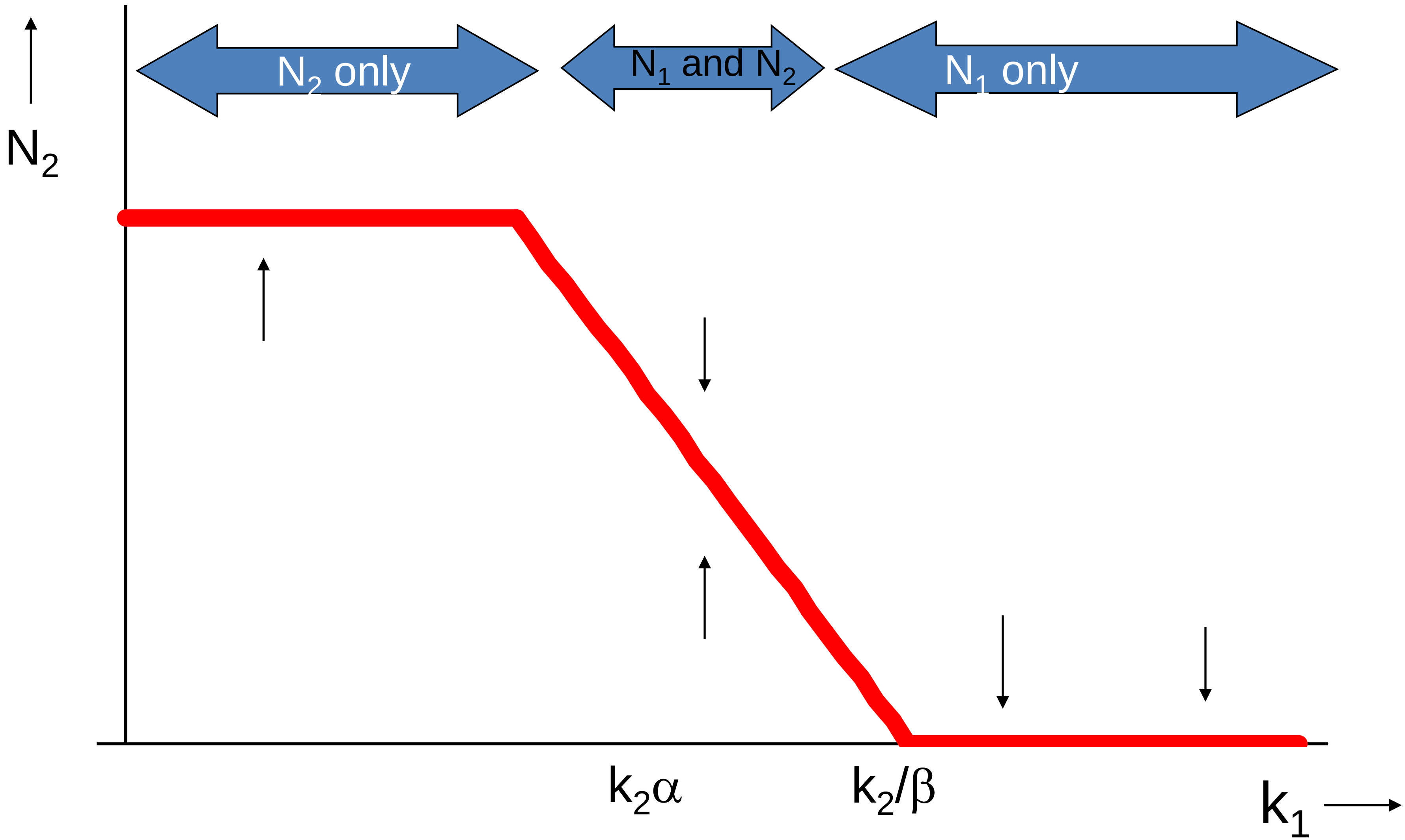


Alternative stable states

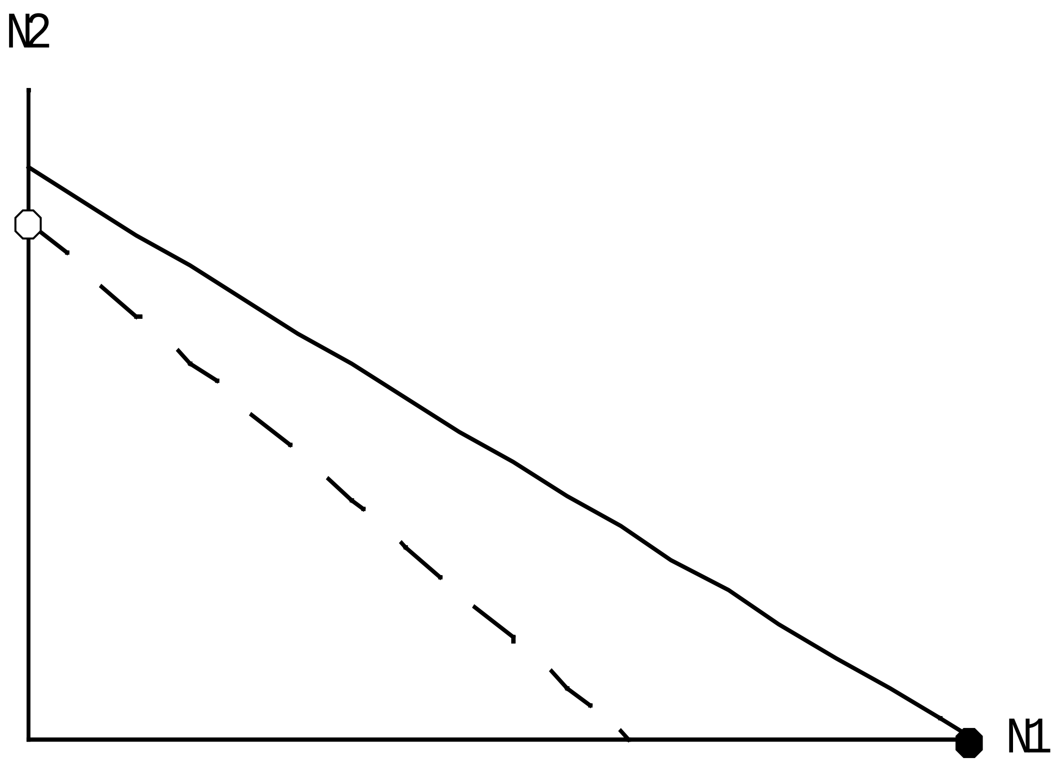
What happens if we change the carrying capacity?



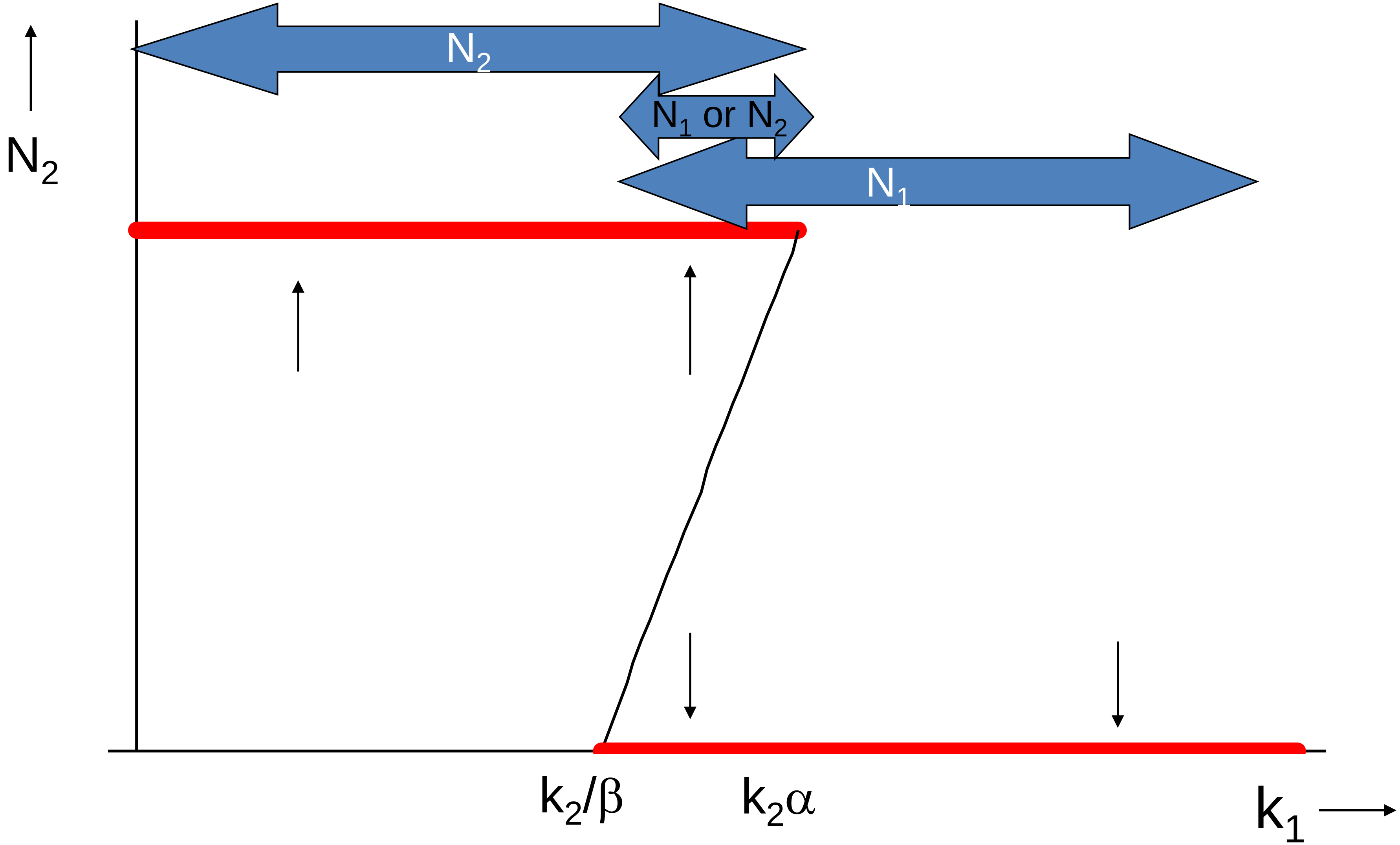
Phase shift



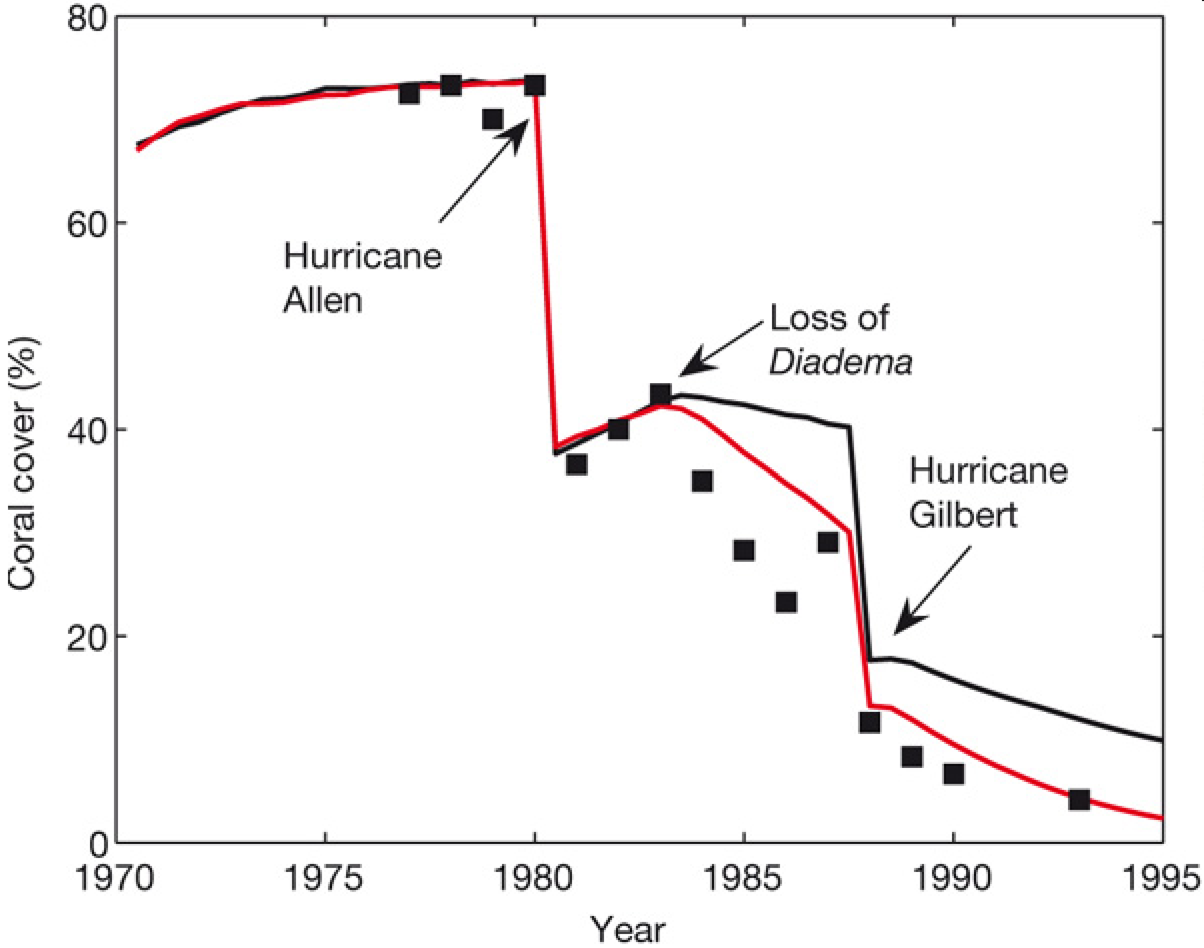
Other option if we change the carrying capacity (for different α and β)



Alternative Stable States, Catastrophic transition

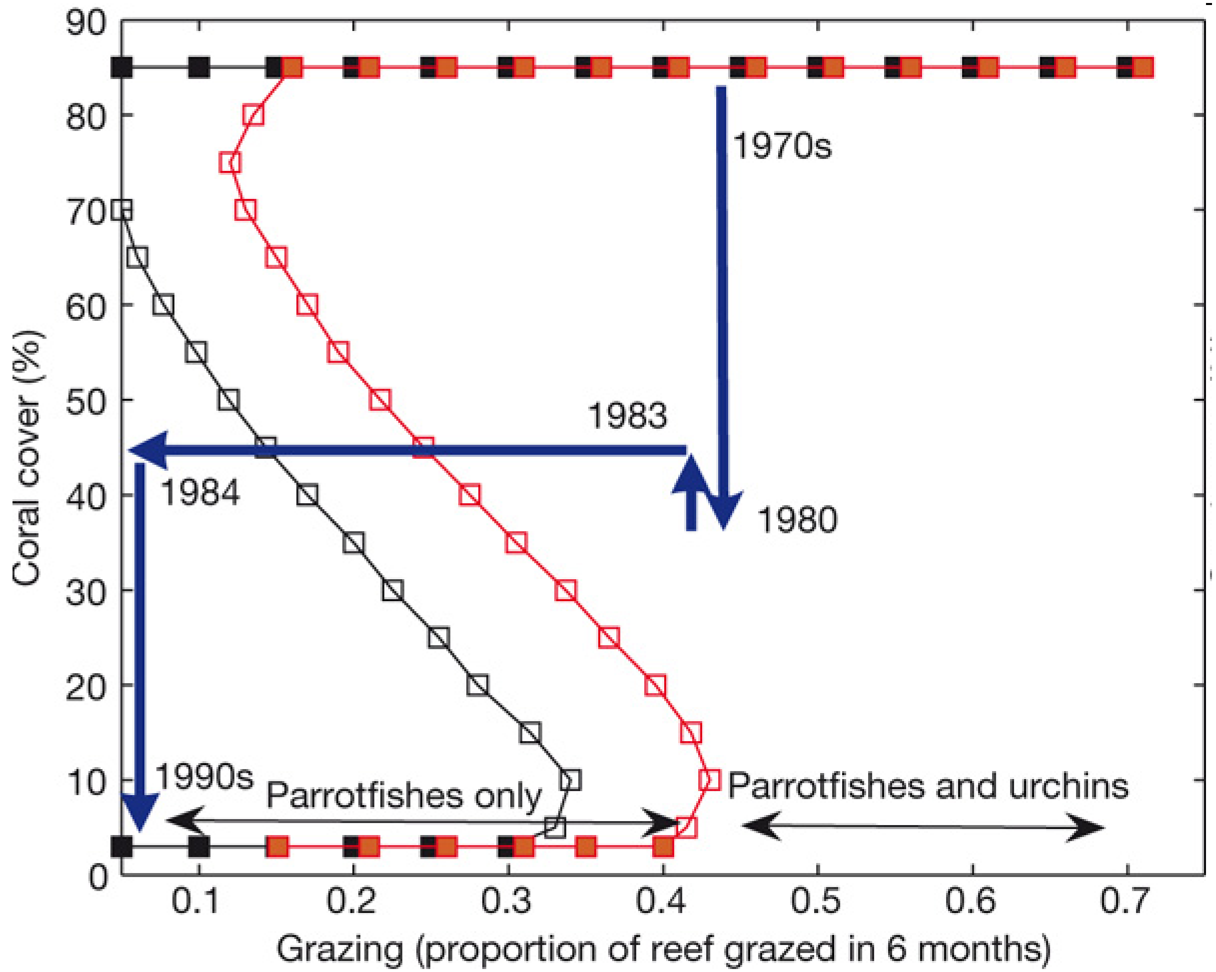


Coral cover in Jamaican reefs

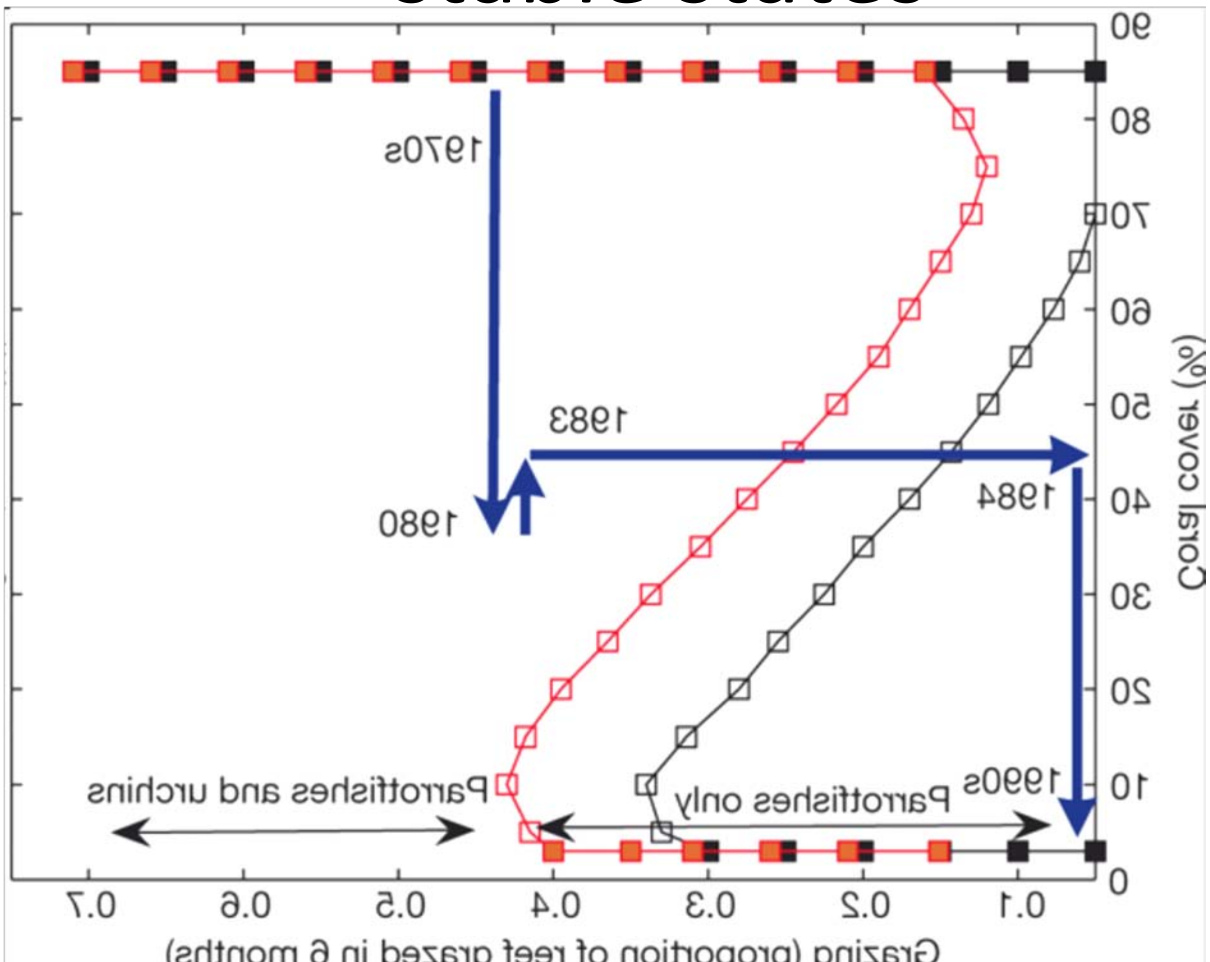


- Predictions are denoted by lines and empirical data are
denoted by black squares

Data explained using alternative stable states



Data explained using alternative stable states

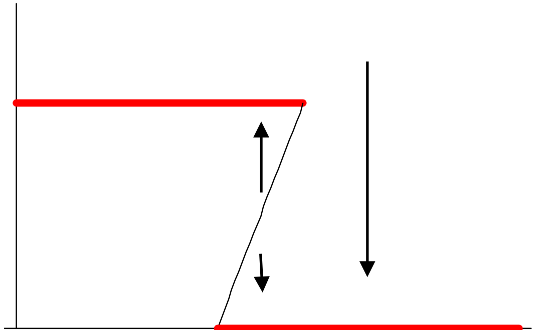


Coral reef recovery

- In the early 1980’s Caribbean reefs experienced a sudden shift from coral dominated reefs to reefs with substantial macroalgae populations
- This followed a time of chronic fishing of herbivores, hurricane damage and a die-off of *Diadema antillarum* in 1983
- Although *Diadema* beginning to return in some places, reef recovery is patchy and many reefs still have not recovered to previous levels of coverage

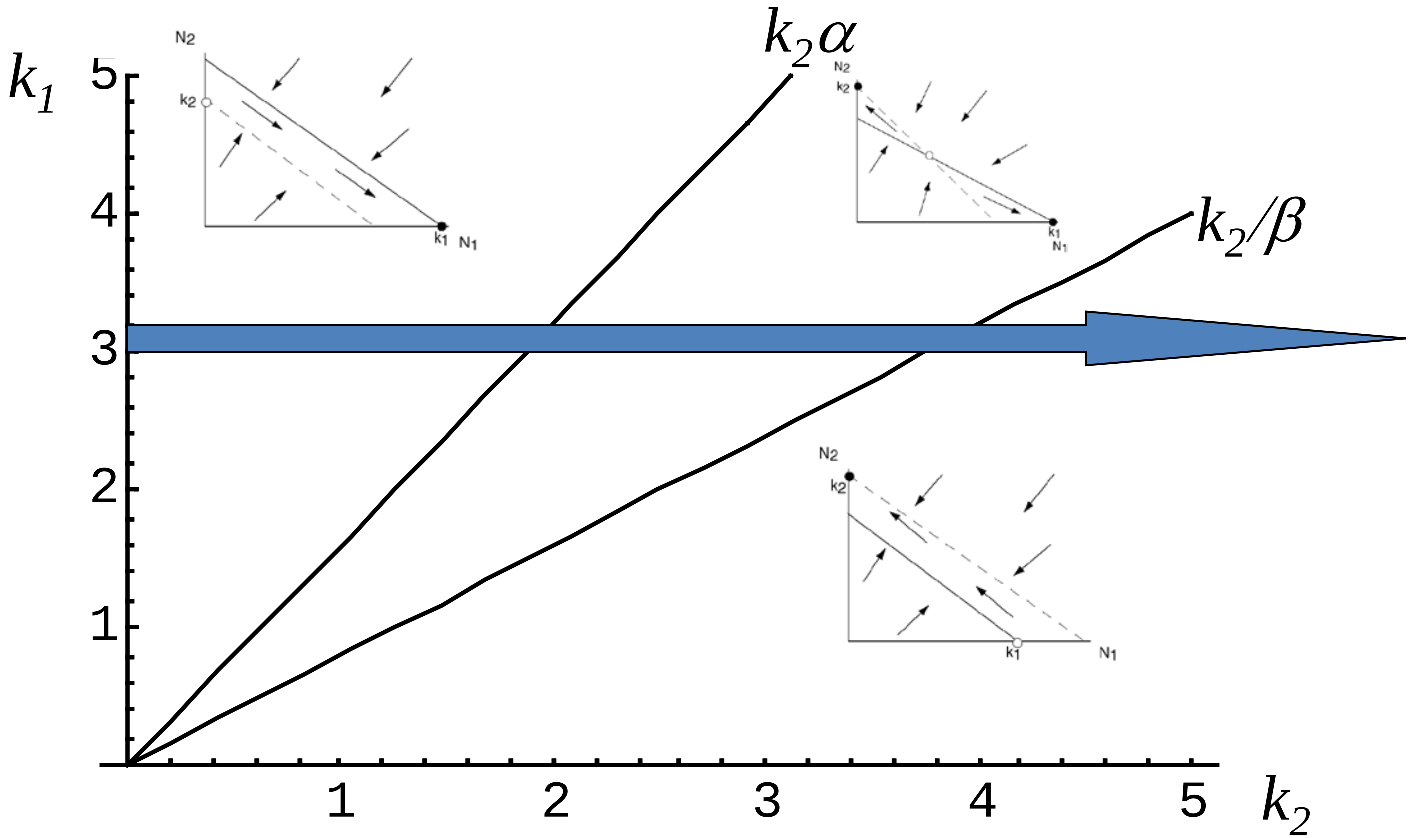
Catastrophic transitions: management implications

- If coral reefs, or other ecosystems have alternative stable states, this has important management implications.
- In general, prevent large perturbations and manage so that the basin of attraction of the desirable state is largest
- For instance, through limiting overfishing of herbivores



Generic situation

- Codim 2 Bifurcation diagram of LV competition model



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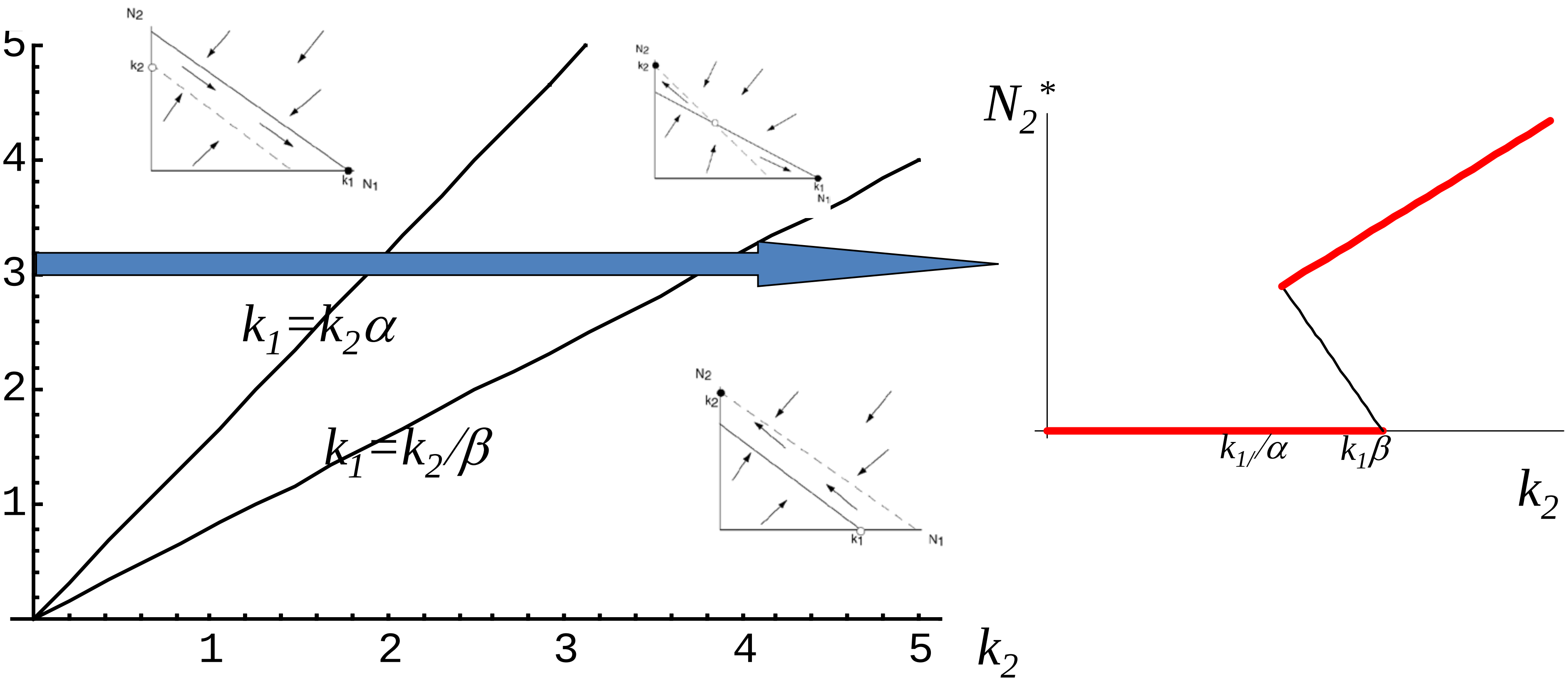
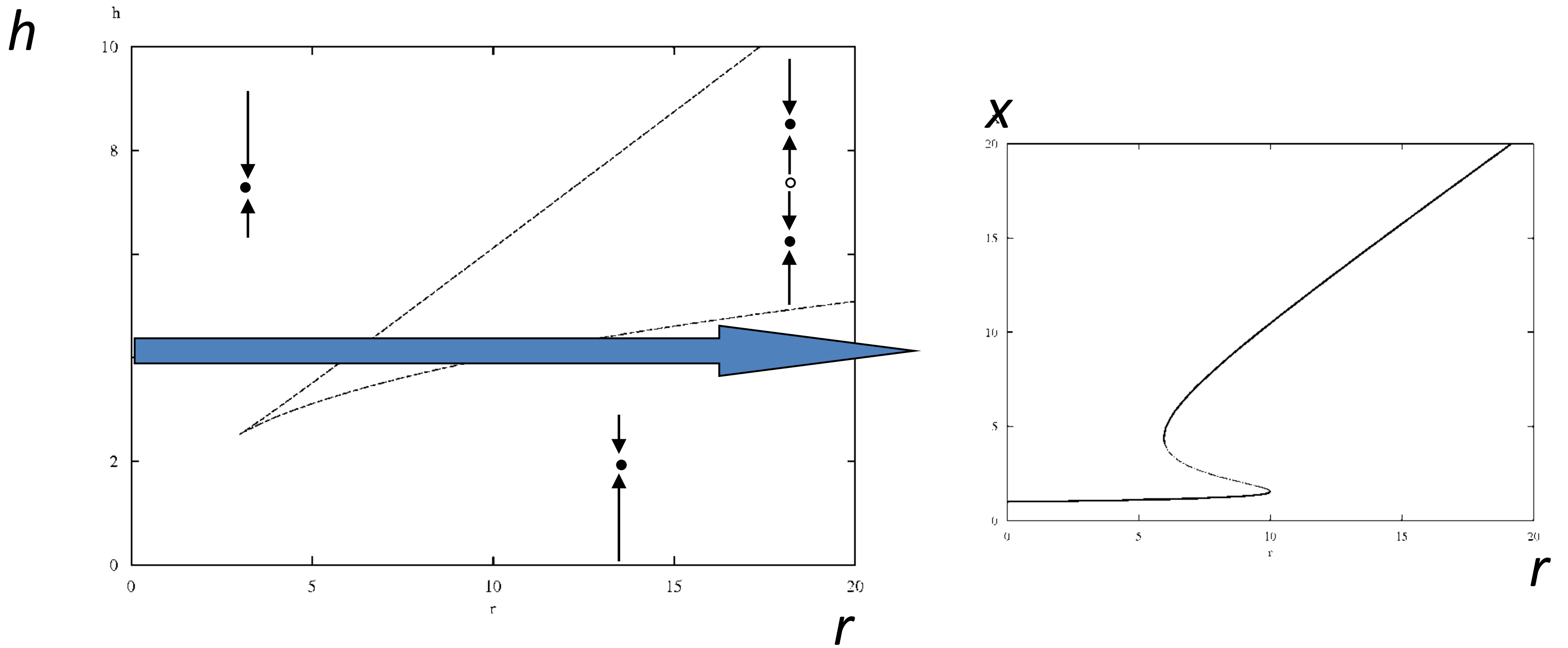
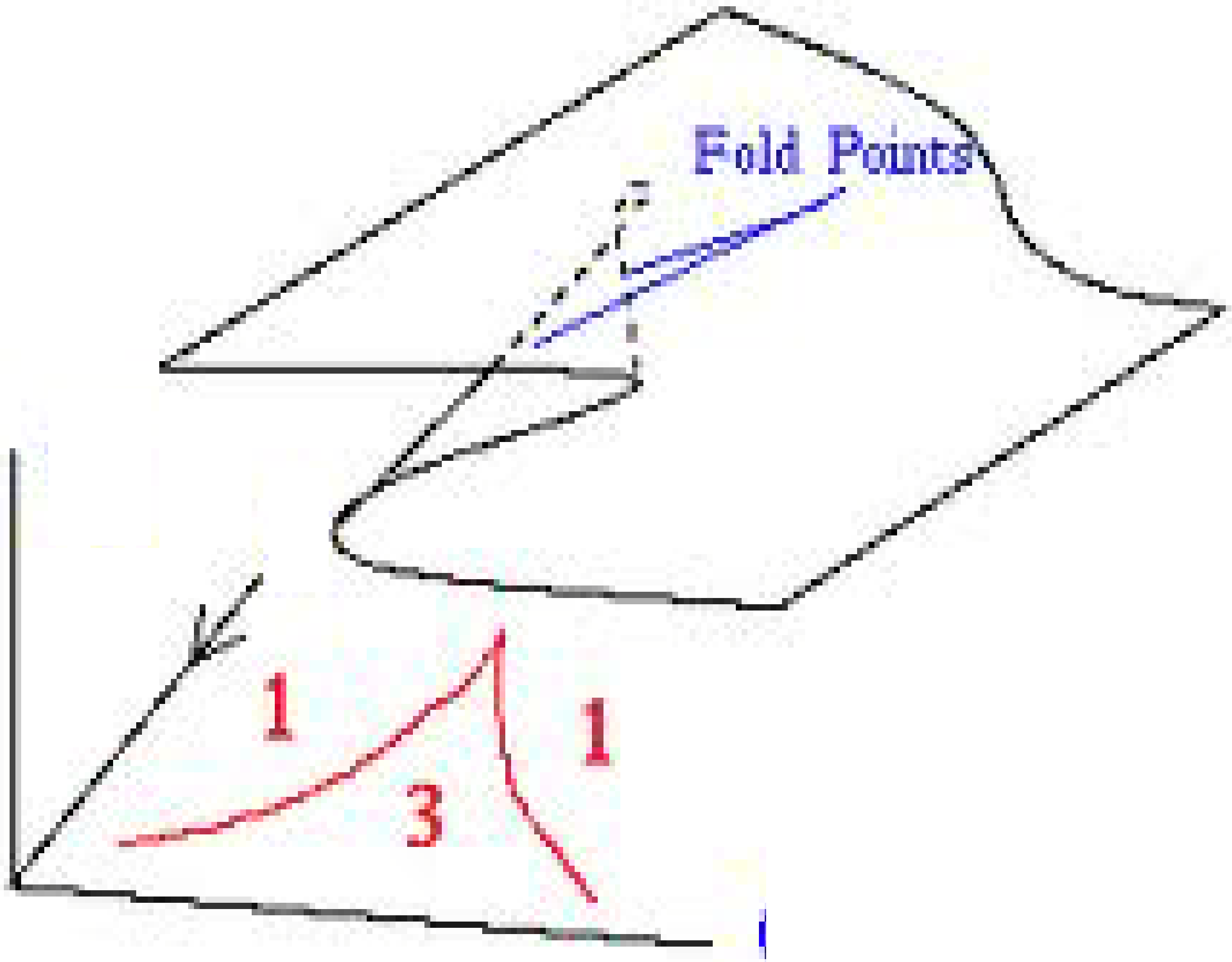


Generic situation

- Generic codim 2 Bifurcation diagram
- This is cusp bifurcation



Generic situation



Alternative stable states are found in vary different ecosystems:

- Lakes
- Deserts
- Woodlands
- Fisheries
- Coral reefs

See review Scheffer in Nature 2001

Evidence

- Although a compelling story, it is not universally accepted that the decline of coral reefs is caused by alternative stable states.
- One of the problems that it is hard to show in a real ecosystem that there are multiple stable states
- See See Mumby et al. Oikos (2013), also Dudgeon et al. MEPS (2011)

Evidence

- In general, it is difficult to show this conclusively, as
  - Catastrophic shifts are rare events
  - Statistic methodology underdeveloped
- to demonstrate alternative stable states you need to
  - Have repeated shifts
  - Show it plausible there are alternative stable states (fit data using models)

Bee decline

- Insects pollinate about 75% of crop species and enable reproduction in up to 94% of wild flowering plants
- One in 3 mouthfuls of food depends on bee pollination

Bee decline

- Pollinators are declining in many regions:
- USA: 59% loss of colonies 1947-2005
- Central Europe: 25% loss   1985-2005
- UK: 10 of the 16 bumblebee species are declining, 6 are stable/increasing

Bee decline

- The reasons for bee decline are unclear and hotly debated.
- Parasites, diseases, land use, invasive species, climate change and pesticide use have all been suggested as causes
- None has been identified as a sole cause.

Why the cause of bee decline is so difficult to find

Agent	CCD (n = 30)	Non-CCD (n = 21)	Total (n = 51)
IAPV	25 (83.3%)	1 (4.8%)	26 (51.0%)
KBV	30 (100%)	16 (76.2%)	46 (90.2%)
N. apis	27 (90%)	10 (47.6%)	37 (72.5%)
N. ceranae	30 (100%)	17 (80.9%)	47 (92.1%)

Prevalence of 4 diseases in collapsing colonies

Cox-Foster et al. Science (2007): 318, 283-287

Nature, 16/10/2013 highlights a paper:

ENVIRONMENTAL SCIENCE

Why bee colonies collapse

Effects of exposure of sublethal pesticides

- A number of models was made. One of the models has a death rate that has positive density dependence
- The positive death rate reflects that larger colonies survive better because these colonies function better (e.g forage better, are better at temperature control, hygiene, etc.)
- This creates alternative stable states (an Allee effect)

Bryden et al. Ecology Letters (2013)

Effects of exposure of sublethal pesticides

$$\frac{dS}{dt} = bN - \frac{\mu}{N+\phi}S - \beta S$$

$$\frac{dI}{dt} = \beta S - \frac{\mu}{N+\phi}I - vI;$$

birth
death
impairment
death through pesticide

S: healthy bees

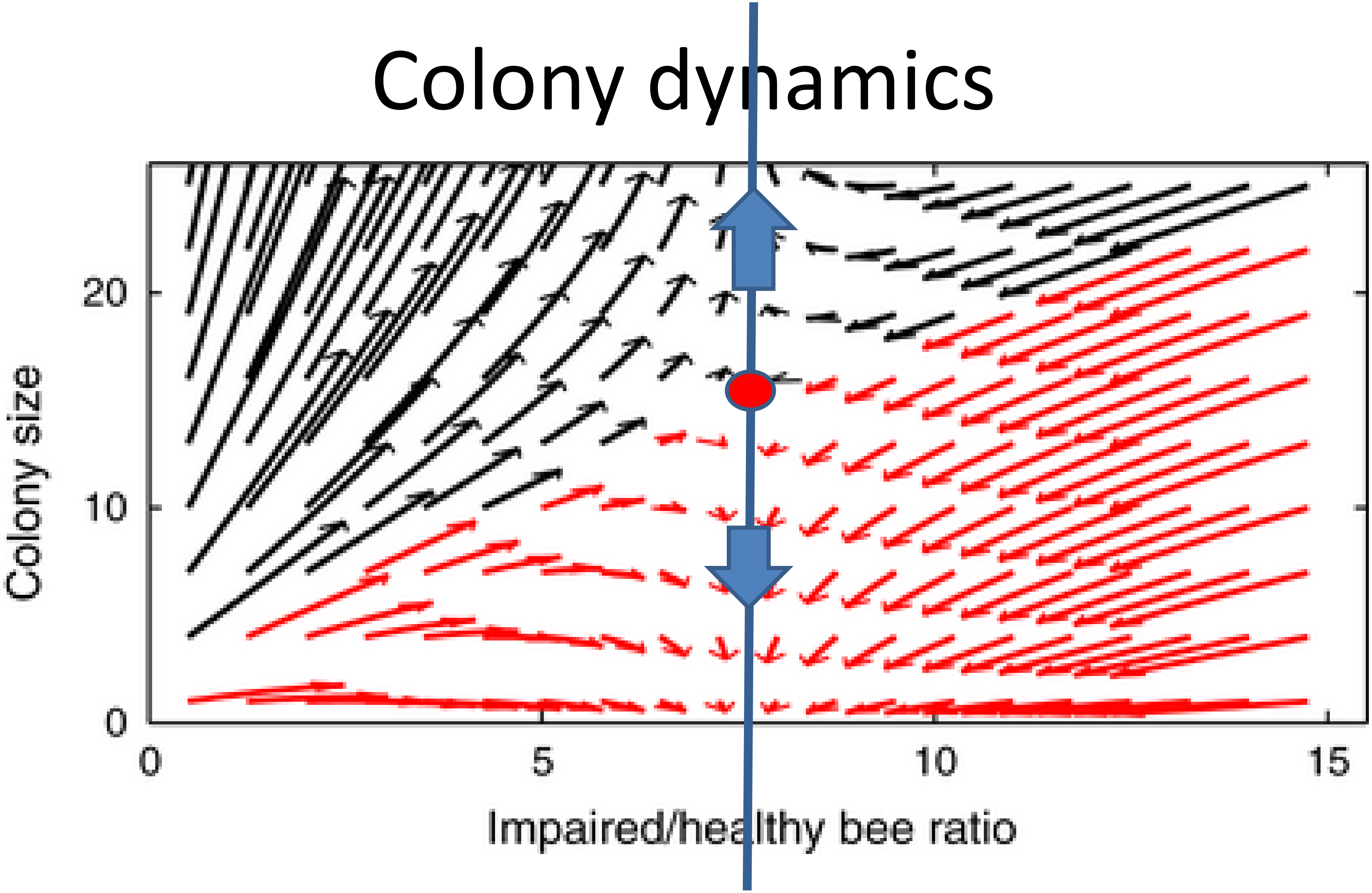
I: bees impaired by pesticide

N:S+cI: effective colony size

Note: per capita death rate density dependent.

Bryden et al. Ecology Letters (2013)

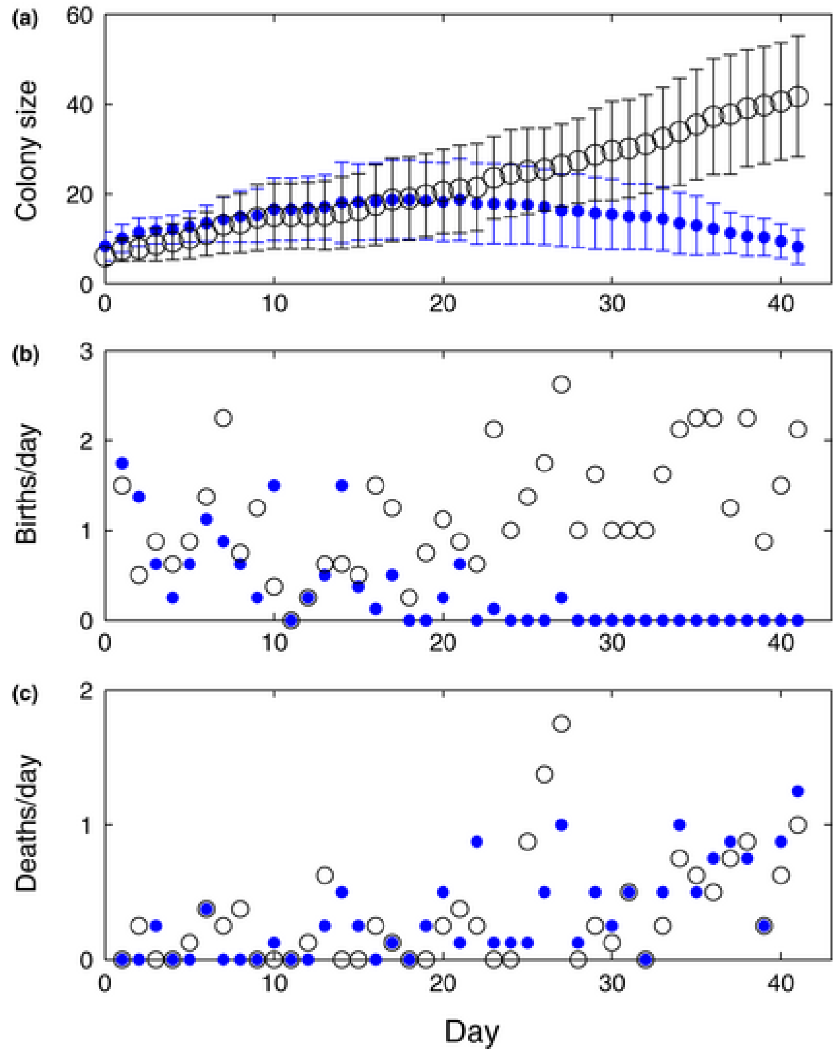
Colony dynamics



Bryden et al. Ecology Letters (2013)

Effects of exposure of sublethal pesticides

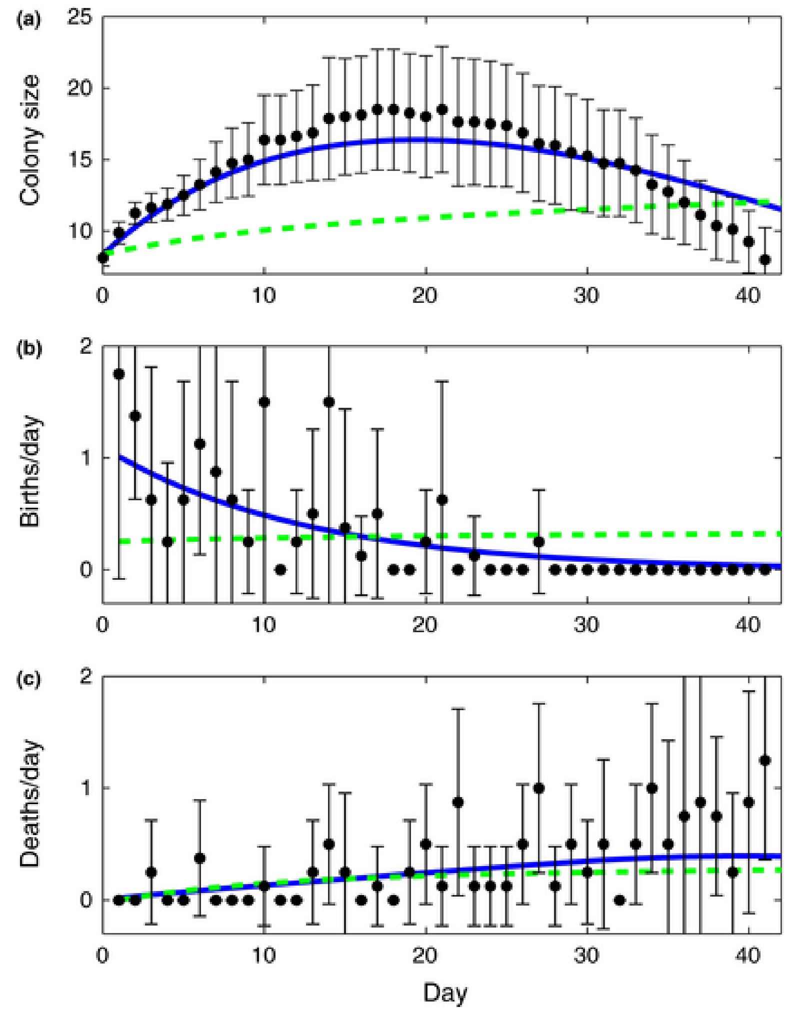
- Colonies were exposed to sublethal pesticide doses (blue). Control (grey) colonies do not fail



Bryden et al. Ecology Letters (2013)

Effects of exposure of sublethal pesticides

- This model (blue line) fits the data best, and better than a model with a linear death rate
- Note: as the colony declines the total death rate increases



Bryden et al. Ecology Letters (2013)

Effects of exposure of sublethal pesticides

Table 2 Summary of the models tested against the treated bumblebee colonies

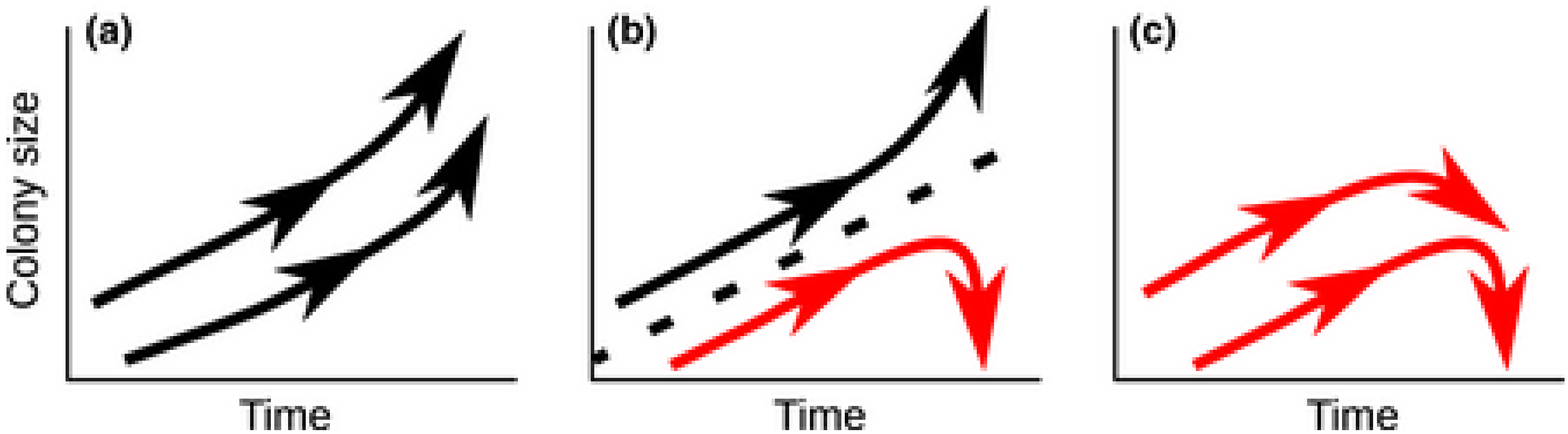
Model	Log likelihood	AIC	Akaike Weight
SLS	−418	852	1
Khoury	−510	1034	0
LA Model	−446	904	0
SLS variant	−437	888	0

The table shows, for each model, the maximum log likelihood found together with calculated Akaike Information Criteria (AIC) values and Akaike weights. There is essentially no support (Burnham & Anderson 2002) for the Khoury Model, SLS Variant or LA Model compared with the SLS Model.

- A number of models was made. The one with the best fit is assumed to be the one that is most correct

Bryden et al. Ecology Letters (2013)

Colony dynamics



Less pesticide

The model predicts that for intermediate pesticide exposure, colonies can grow, or fail. We think this can explain the result of Cox-Foster (2007)

Any stress (including disease) could cause alternative fates

Agent	CCD (n = 30)	Non-CCD (n = 21)	Total (n = 51)
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Prevalence of 4 diseases in collapsing colonies

Cox-Foster et al. Science (2007): 318, 283-287

Lake Myvatn, Iceland

Midges can be highly abundant

Swarms of *Tanytarsus gracilentus*

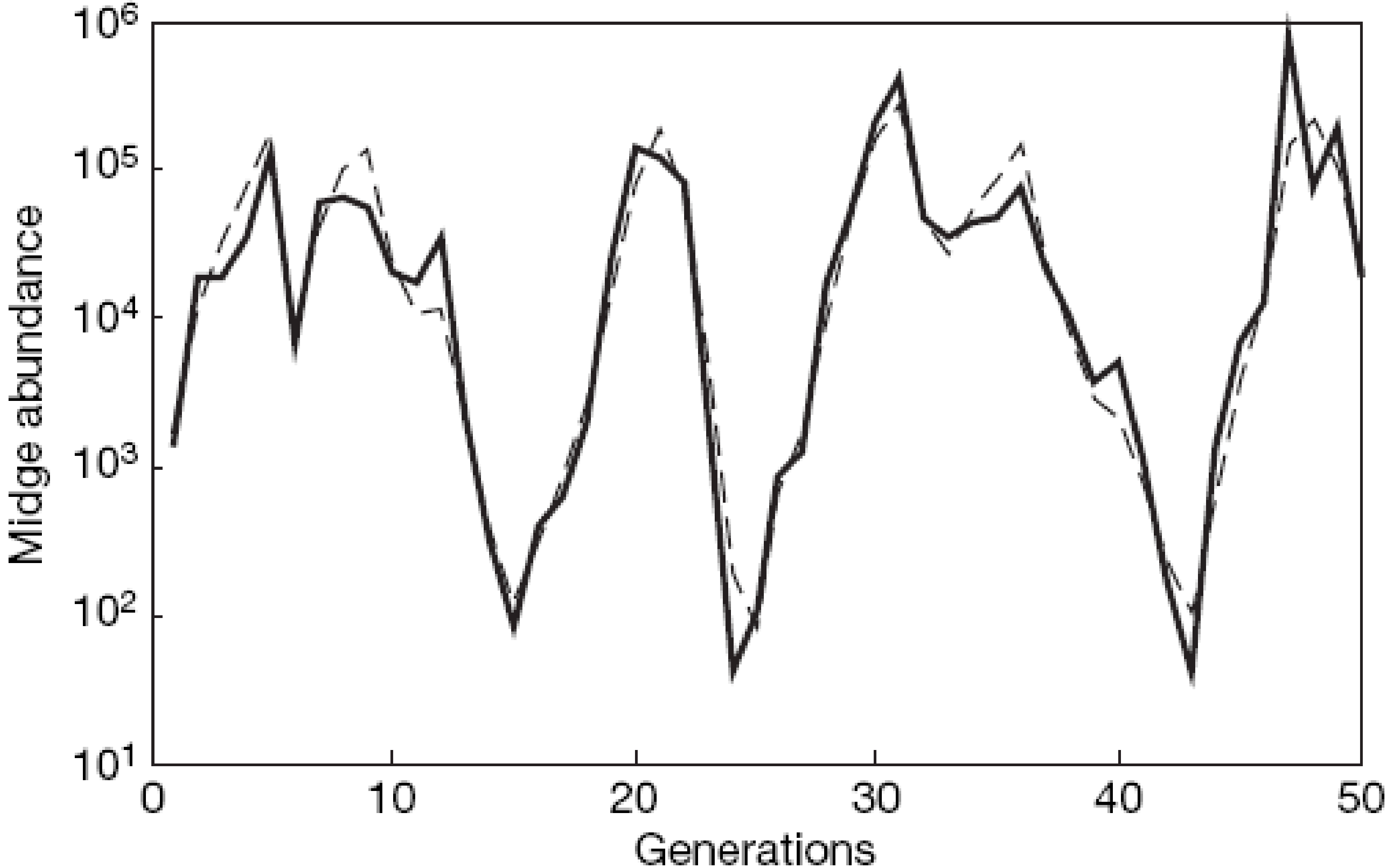
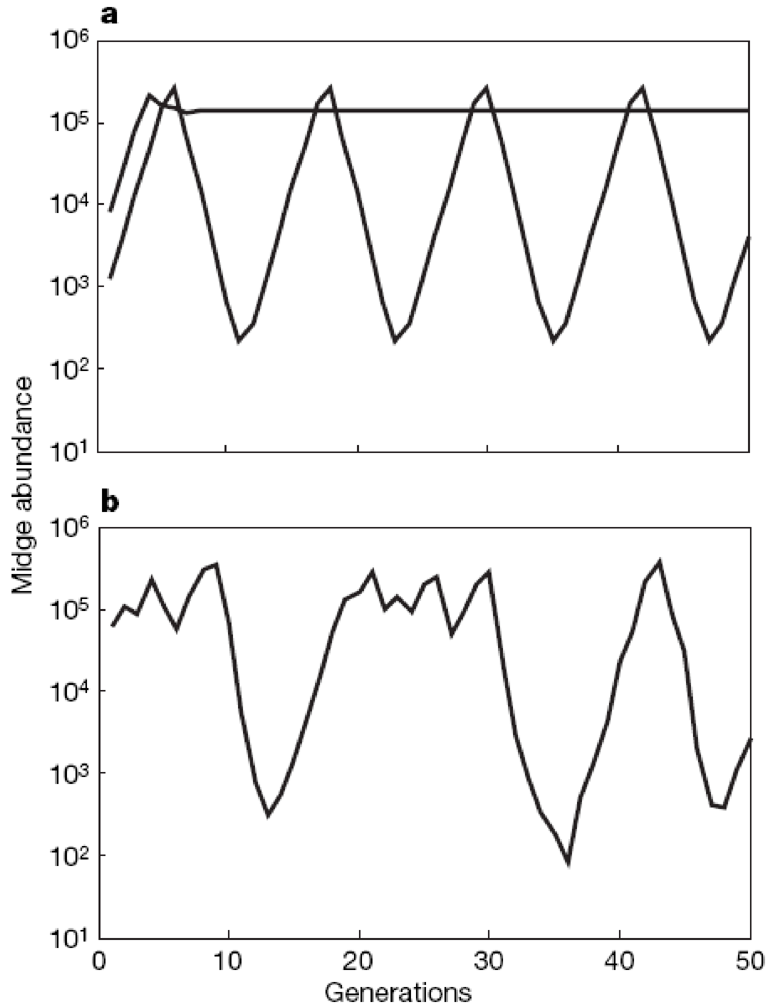


Figure 1 | Population dynamics of *T. gracilentus* in Myvatn.

From Ives et al. *Nature* 2008

Possible explanation:
Alternative stable states



Demonstrating existence of alternative stable states

- 3 models are compared
- Only the midge-algae detritus model has alternative stable states
- This is best description given the data

Table 1 | Goodness-of-fit measures for the midge–algae–detritus and alternative models

Goodness of fit	Model		
	Midge–algae–detritus	Gompertz	Lotka–Volterra
Number of parameters*	6	9	9
−2 LL	156.2	174.7	185.5
Total R^2	0.98	0.98	0.97
Prediction R^2 for $\hat{X}(t+1)$	0.74	0.57	0.38
Prediction R^2 for $X(t+1)$	0.53	0.39	0.25

Learning outcomes

- Understand how a change in carrying capacity can bring about a qualitative change
- the difference between a phase transition and catastrophic transition
- Understand the importance for ecosystems, management and conservation
- Appreciate the issues regarding providing evidence for alternative stable states.

Period doubling, chaos

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Back to the logistic

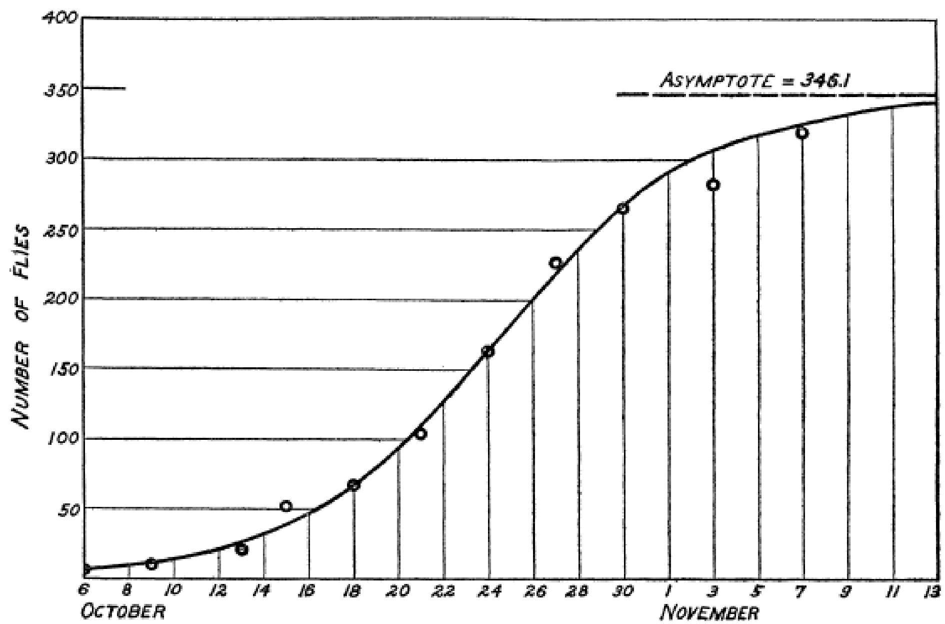


FIG. 9. GROWTH OF AN EXPERIMENTAL POPULATION OF DROSOPHILA
The circles are observed census counts, and the smooth curve is the fitted logistic. (From Pearl (8))

A Drosophila population kept in the lab. Another logistic growth curve from the work of Pearl. (1927) Q. Rev. Biol. 2 532-548.

A quote from Pearl (1927)

- “Many experiments of this type have been performed. The general result is that the population first grows up to a maximum or asymptotic level, …. A striking result, however, is that both during the growth period and thereafter there are violent oscillations of the populations in size, about its mean position as given by the fitted curve. In fact these waves in the size of the population, produced by oscillations in the birth and death rates, are perhaps the most characteristic feature of population experiments of this particular type. It has not so far been possible to devise any method of holding these populations in a steady state at the level of the asymptote, when there is at all times an abundance of fresh food. The population simply waves up and down about an average size. “

Logistic Map

- The discrete logistic model (also called logistic map) is given by

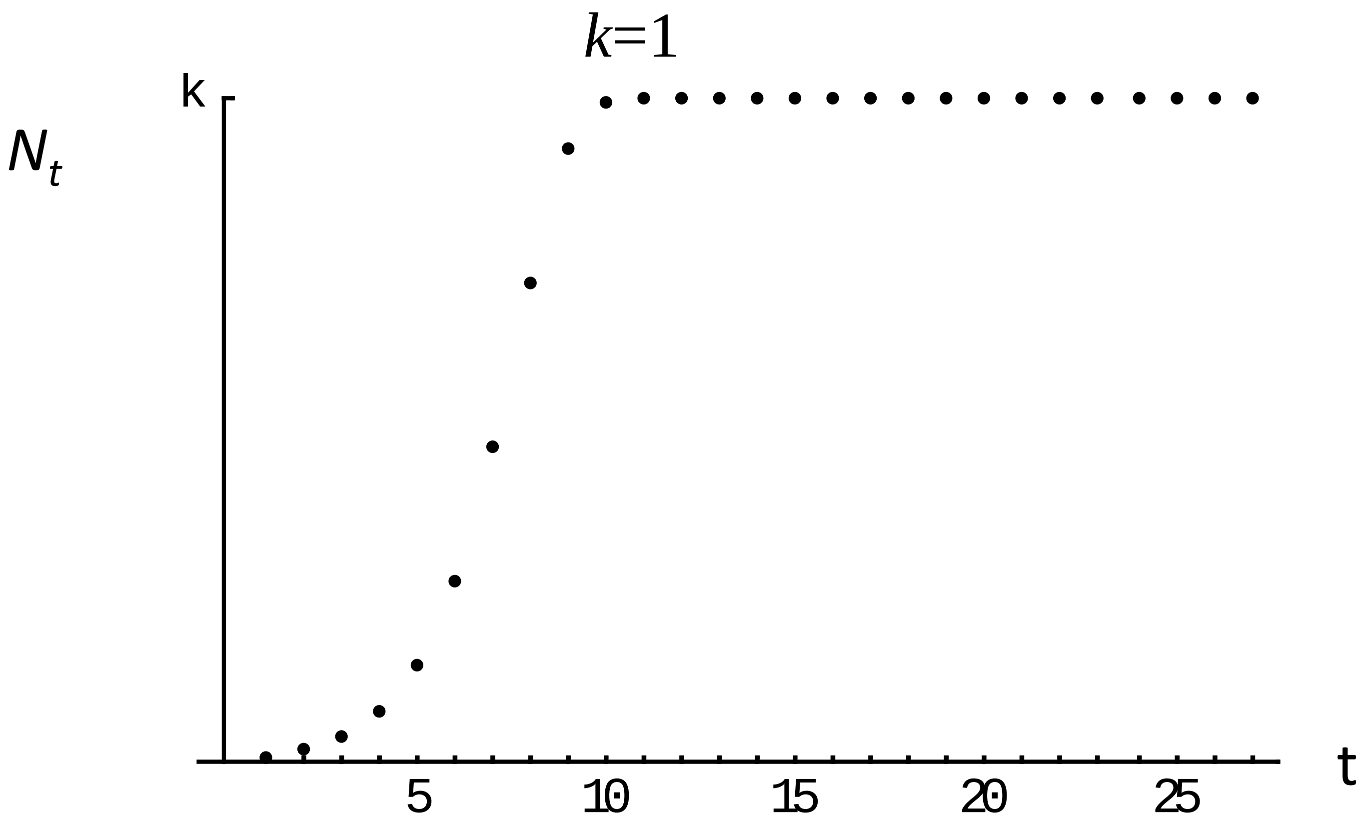
$$N_{t+1} - N_t = r(k - N_t)N_t$$

$$N_{t+1} = N_t + r(k - N_t)N_t$$

with r the maximum per capita growth rate and k the carrying capacity.

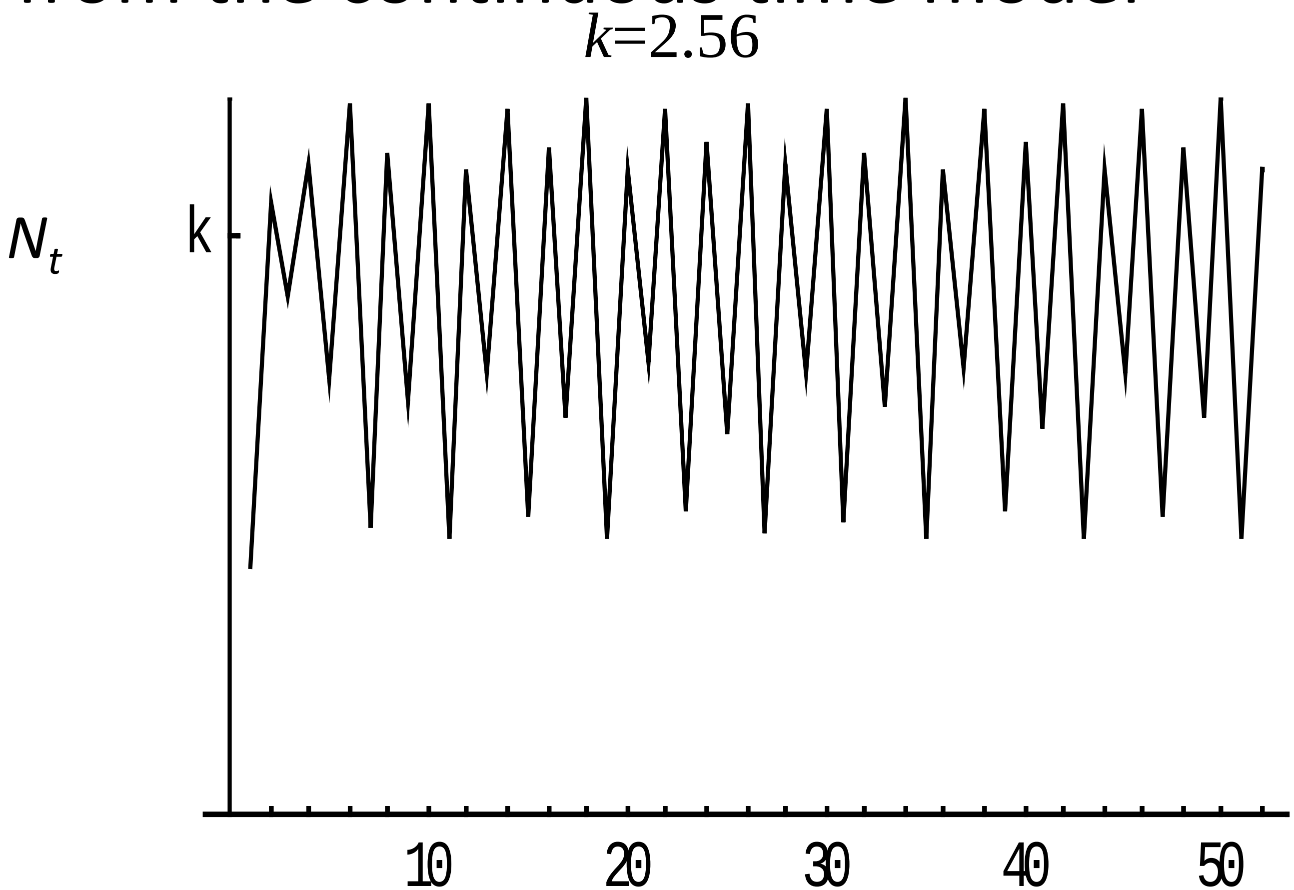
Logistic Map

- For low values of *rk* the dynamics are very similar to those of the continuous growth model. (Value r=1 used in all the pictures)



Logistic Map

- If *rk* is bigger the dynamics begin to differ from the continuous time model



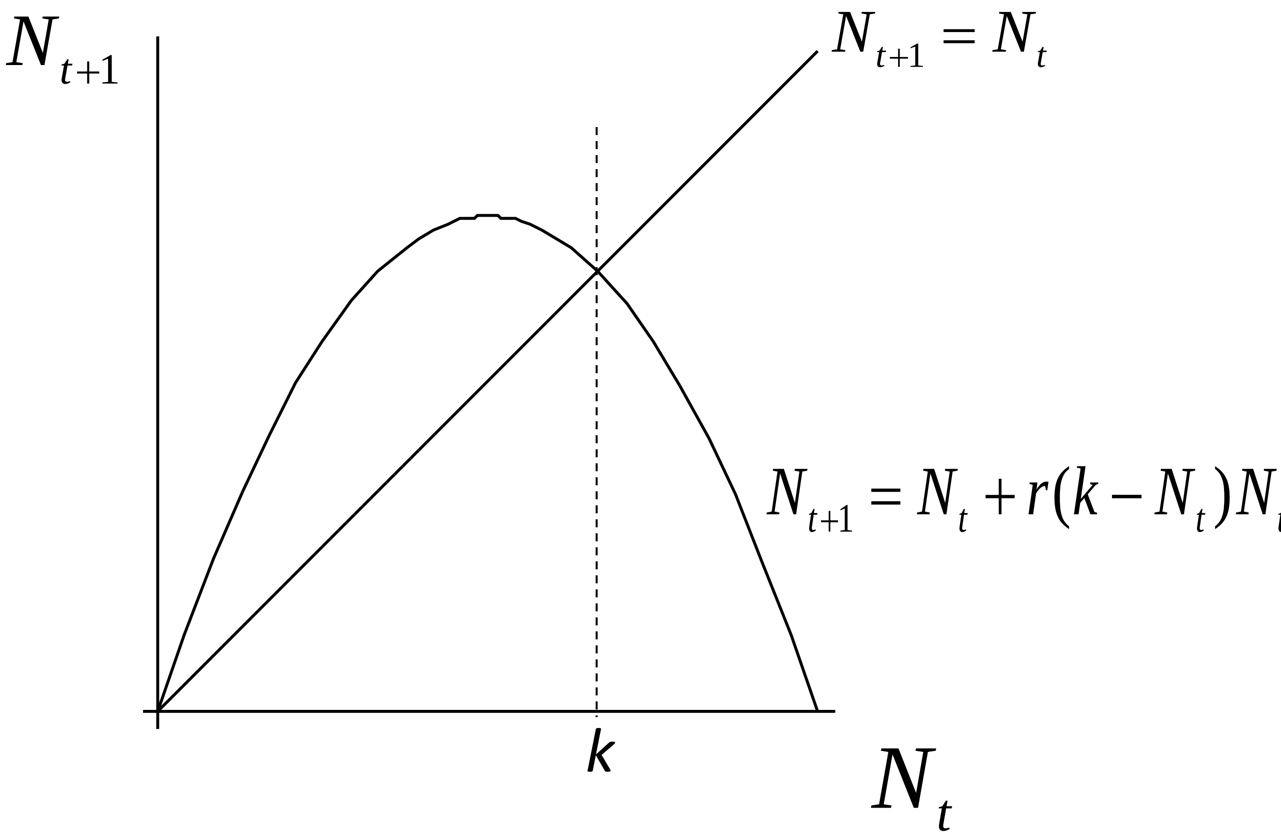
Logistic Map

- The discrete logistic model (also called logistic map) is given by

$$N_{t+1} = N_t + r(k - N_t)N_t$$
$$N_{t+1} = r(k + \frac{1}{r} - N_t)N_t$$
$$N_{t+1} = (rk+1)(1 - \frac{N_t}{k + 1/r})N_t$$

with r the maximum per capita growth rate and k the carrying capacity

Logistic Map : finding the equilibrium



Logistic Map: Stability of the equilibria

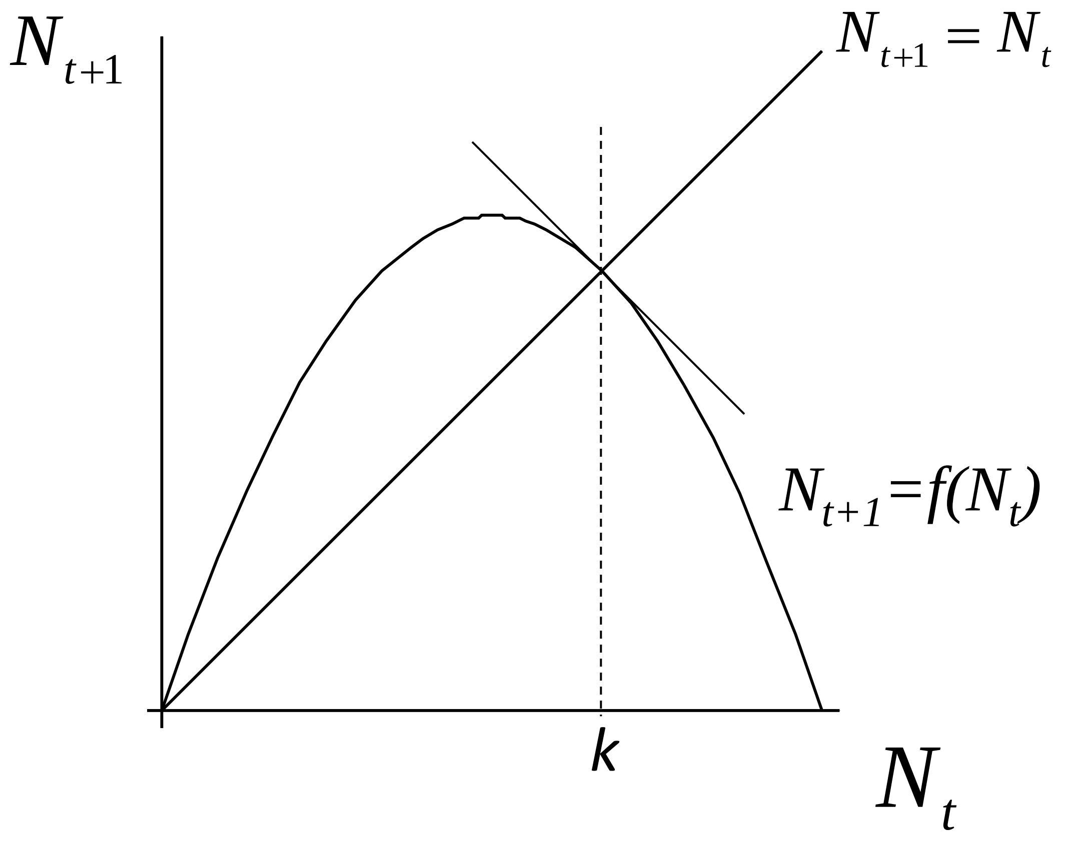
- We study the dynamics close to the equilibrium
- The distance from the equilibrium is $x_t = N_t - N^*$
- The dynamics close to equilibrium are approximately:

$$x_{t+1} = (1 + r(k - 2N^*))x_t$$

- If $N^* = k$: $\quad x_{t+1} = (1 - rk)x_t$
- Note that if the multiplier is <-1 the equilibrium is unstable

- Stable if 0<*rk*<2

Logistic Map: Stability of the equilibrium



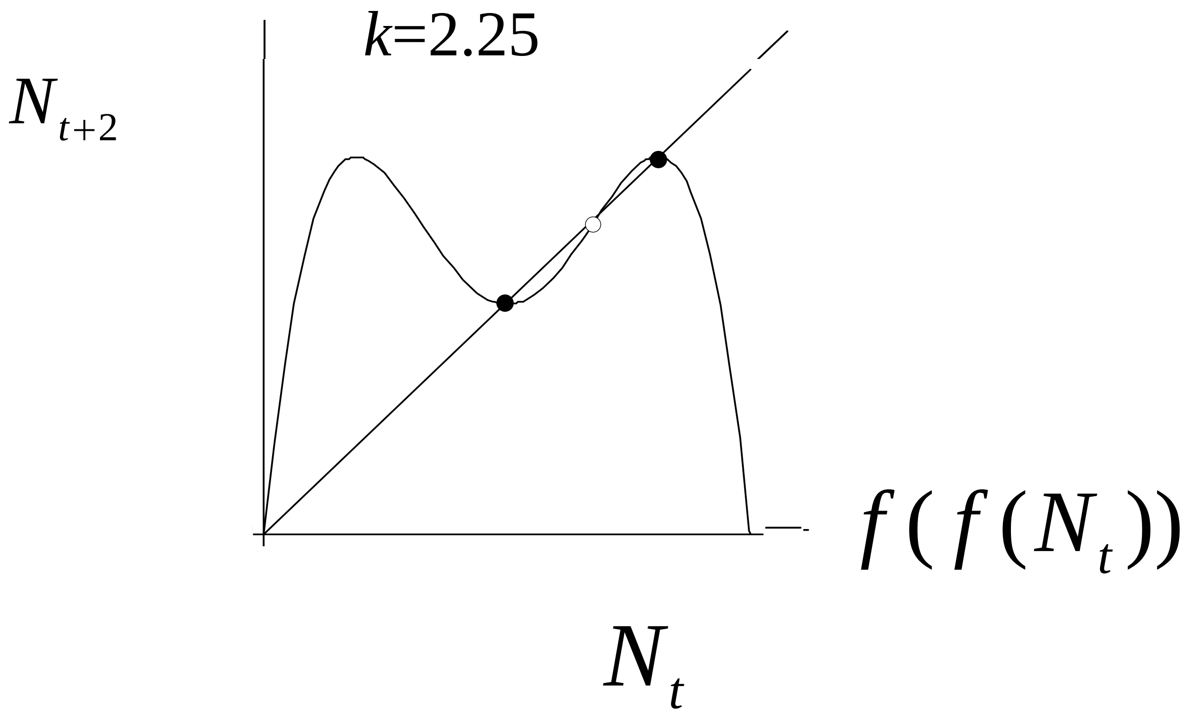
Stability of the equilibrium

- So what happens if the equilibrium loses stability?
- The analysis suggests periodic oscillations. Does this settle into a stable pattern?
- We can find the value for the next step from $N_{t+1}=f(N_t)$
- So after 2 steps we have

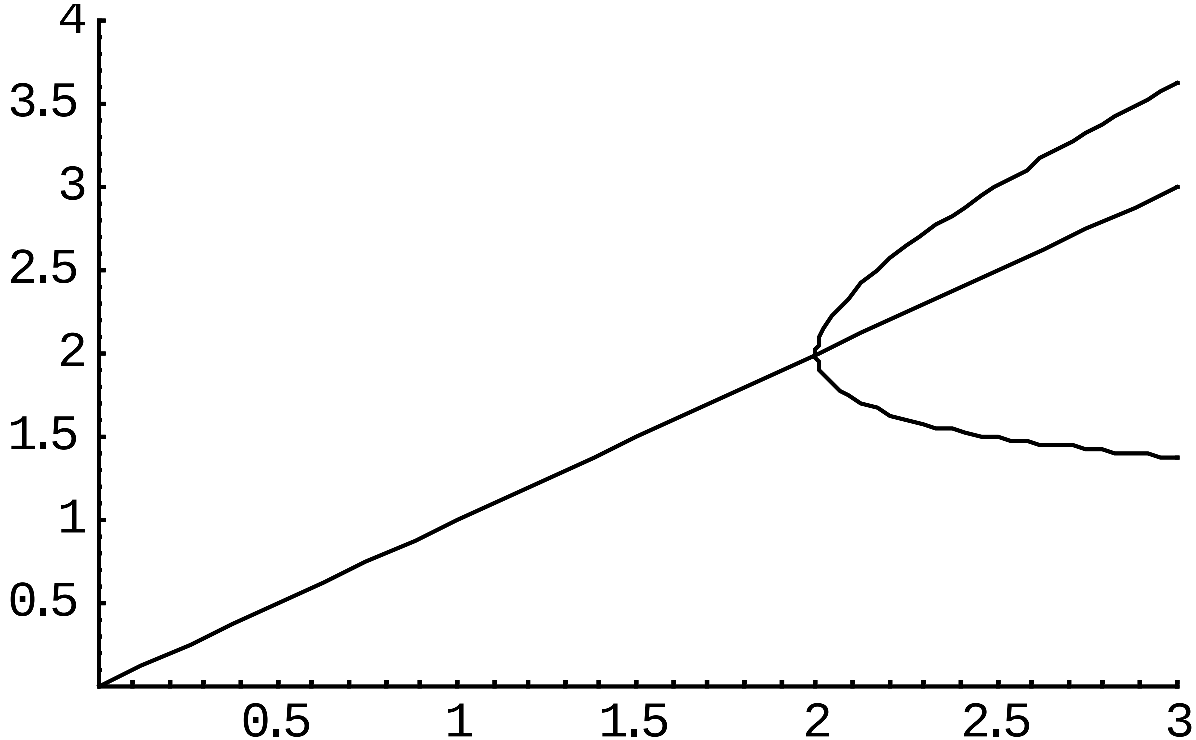
$$N_{t+2} = f(N_{t+1}) = f(f(N_t))$$

- Is there an equilibrium that is reached if we look at every second step?

Logistic Map
Period 2 cycle



Logistic Map
Bifurcation diagram



Logistic Map
Bifurcation diagram

- The equilibrium becomes unstable.
- We can see limit cycles
- We see the sequence

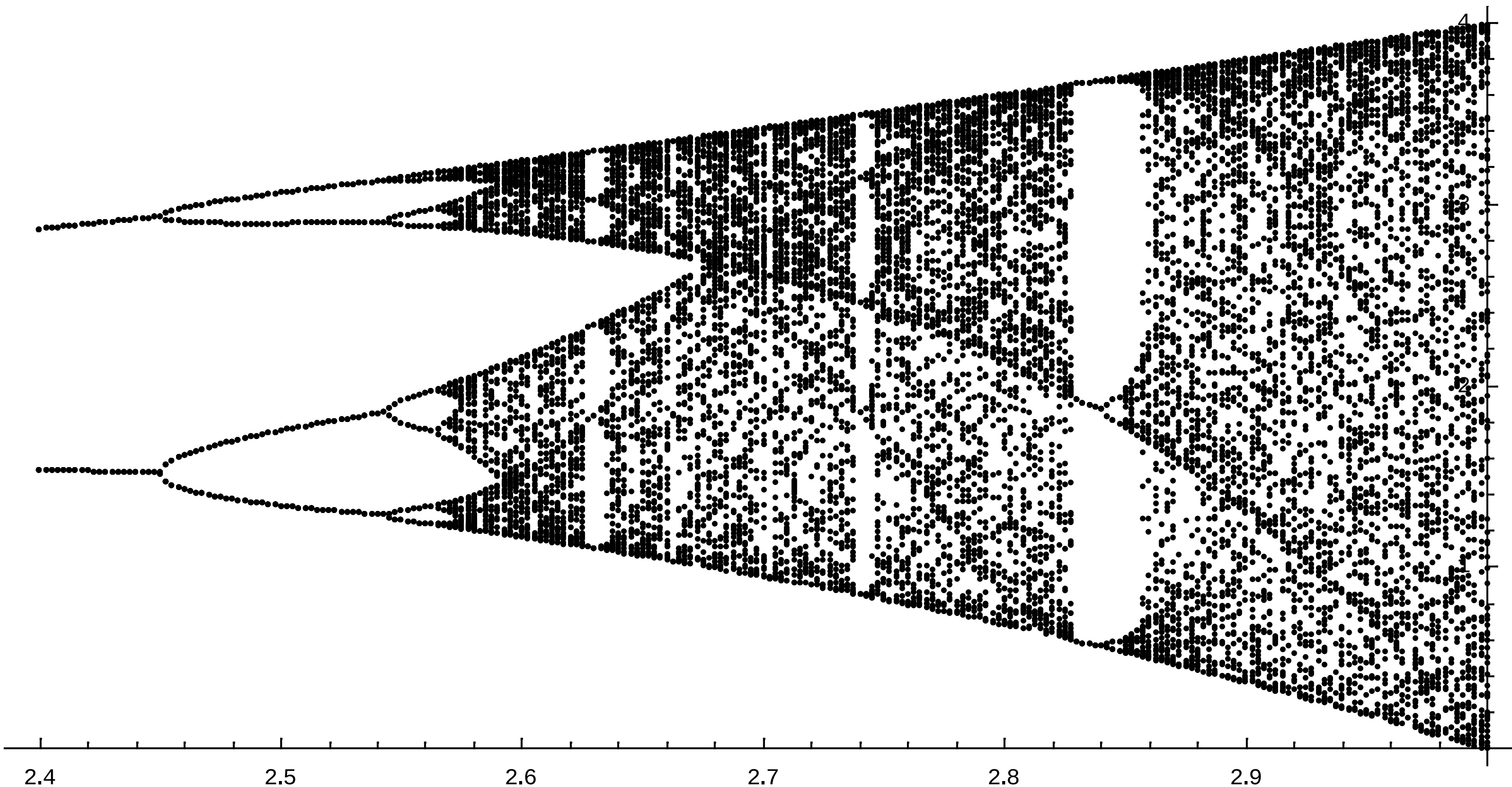
Overcompensation->Period 2 cycles

->Period 4 cycles->Period 8 cycles

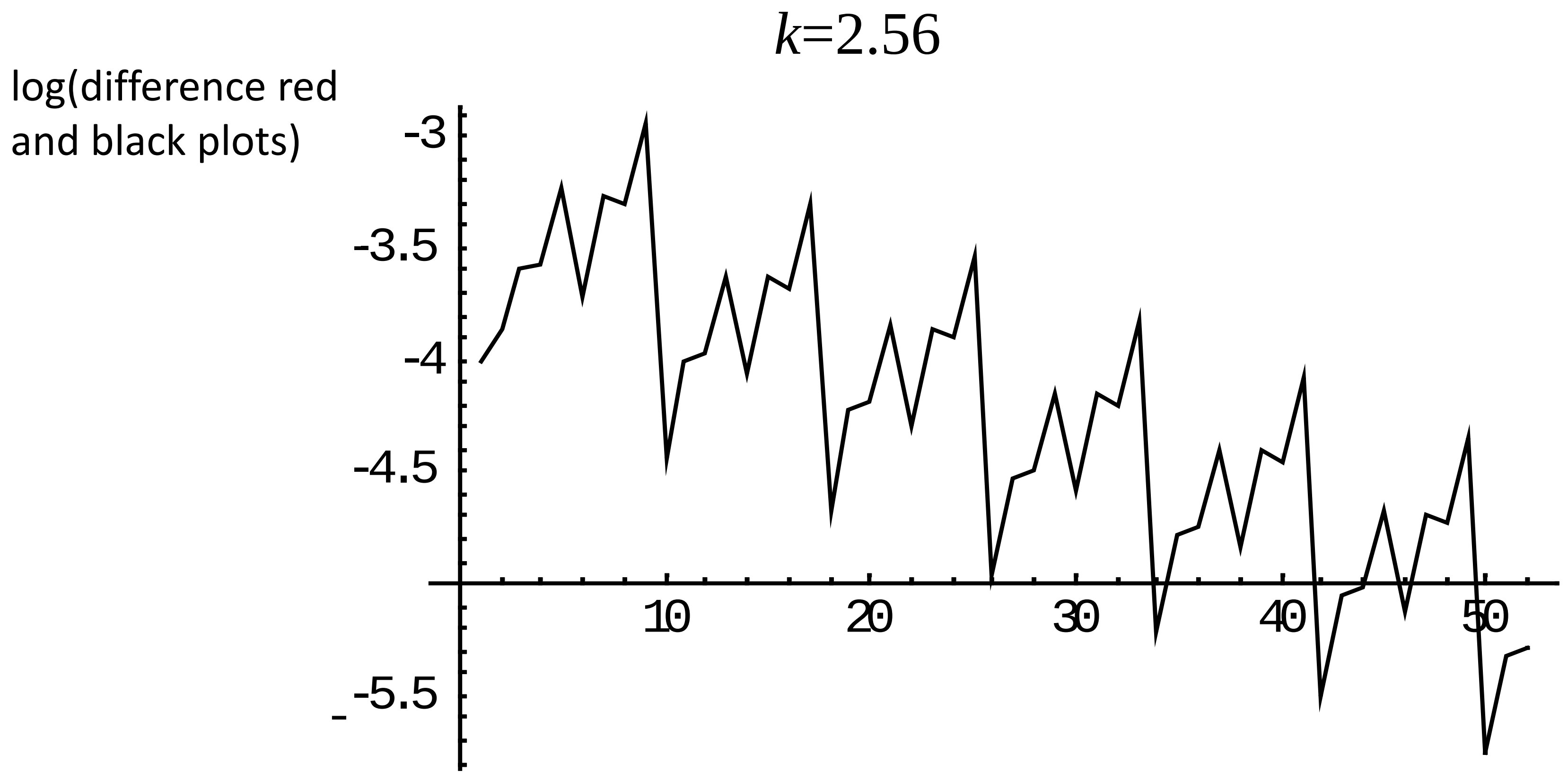
What next?

After going through the period doubling cascade one finds chaos

Logistic Map
Bifurcation diagram

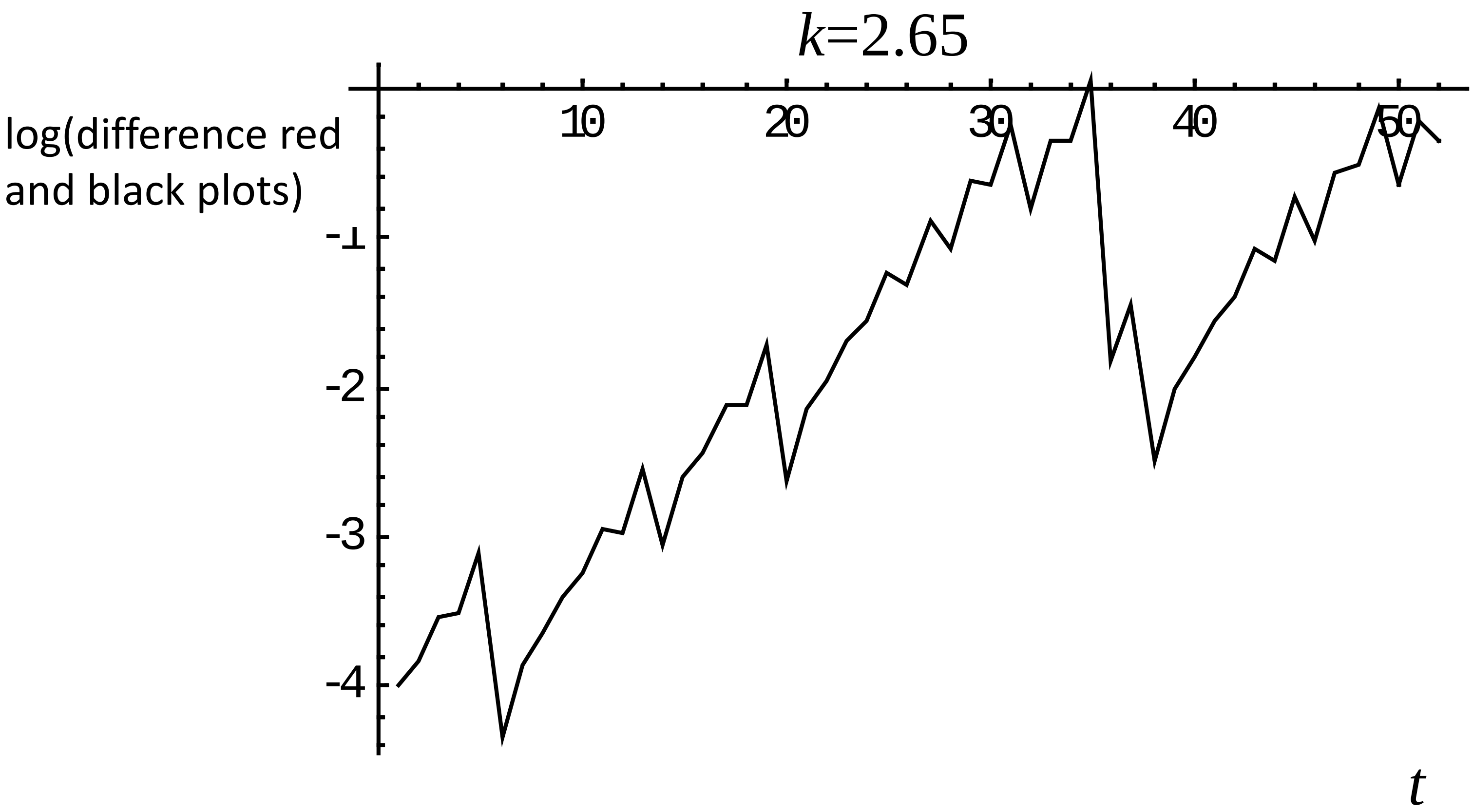


Chaos



k=2.56
log(difference red and black plots)
-3
-3.5
-4
-4.5
-5.5
10
20
30
40
50

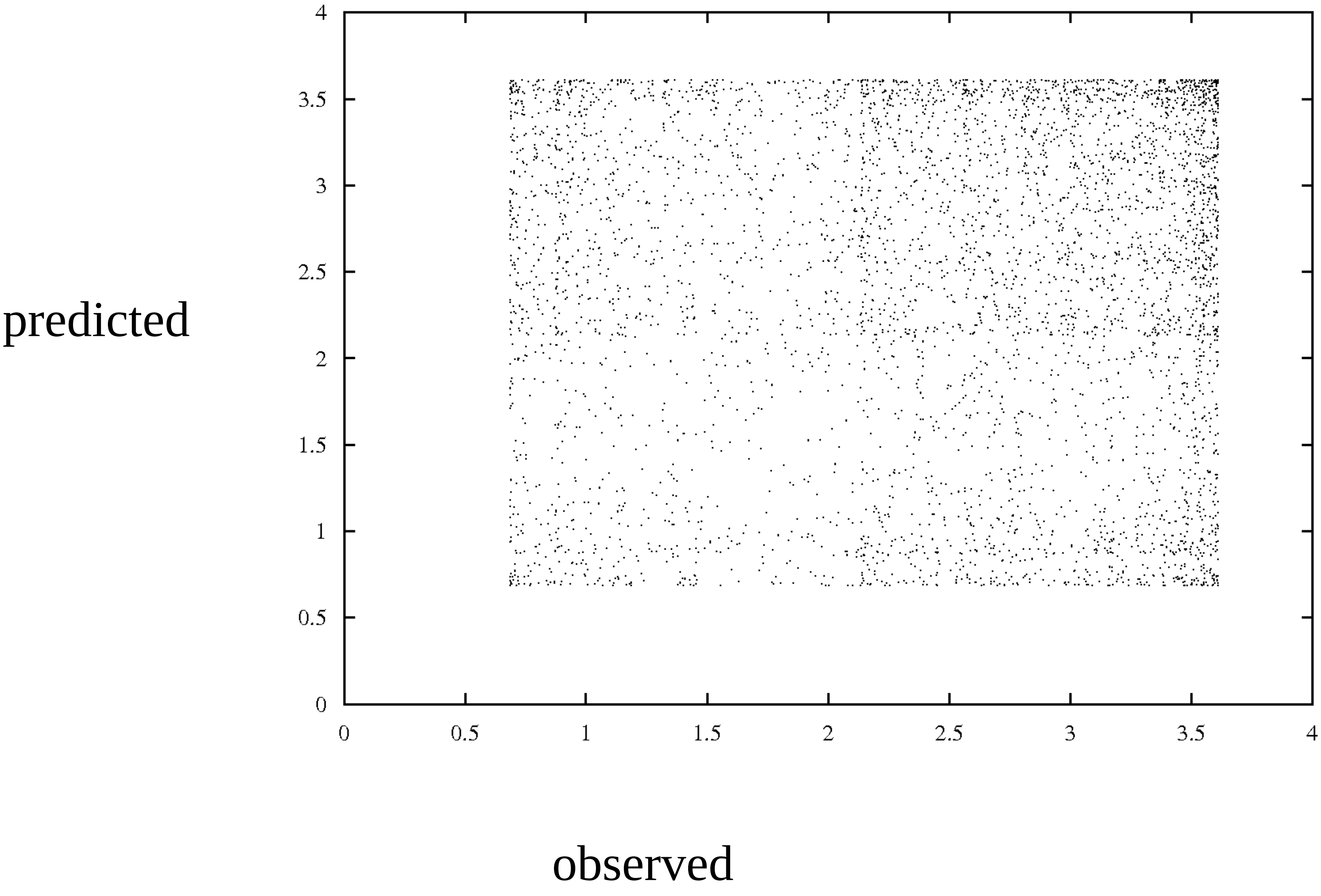
Chaos



Chaos

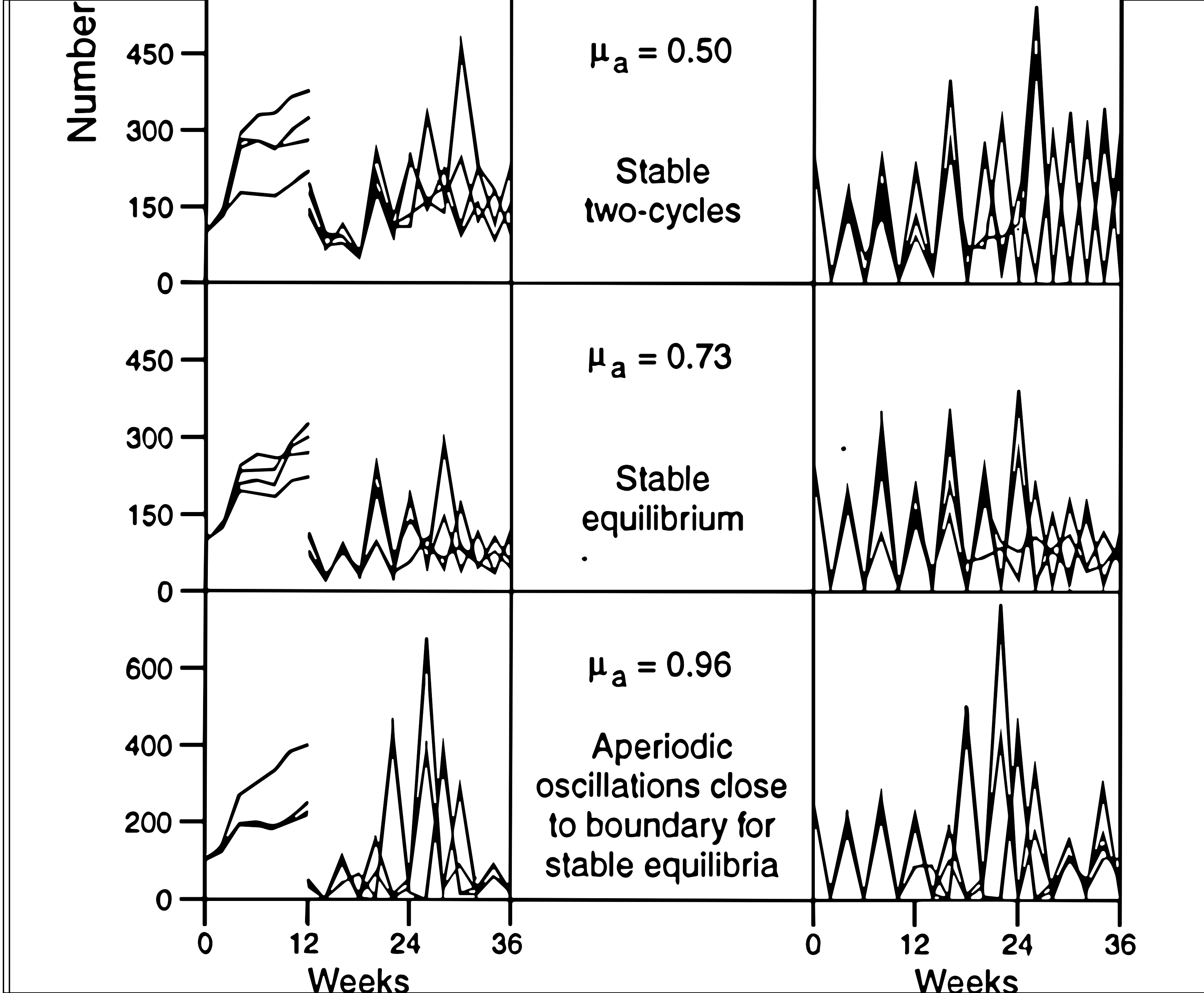
- Why does chaos matter in biology?
- It shows that unpredictability can follow from even if you know exactly how one generation depends on the next
- There are limits to what we can predict, (because we cannot know the present conditions with sufficient precision)

k=2.8



Chaos

- Are population dynamics chaotic?
- There is an example of a single species laboratory system of which the dynamics seem chaotic



Number
450
300
150
0
$\mu_a = 0.50$
Stable two-cycles
$\mu_a = 0.73$
Stable equilibrium
600
400
200
$\mu_a = 0.96$
Aperiodic oscillations close to boundary for stable equilibria
0
12
24
36
Weeks

Chaos

- There are some indications that other systems, with more species are chaotic
- Beninca et al. isolated a marine ecosystem and kept it in the lab. They found:

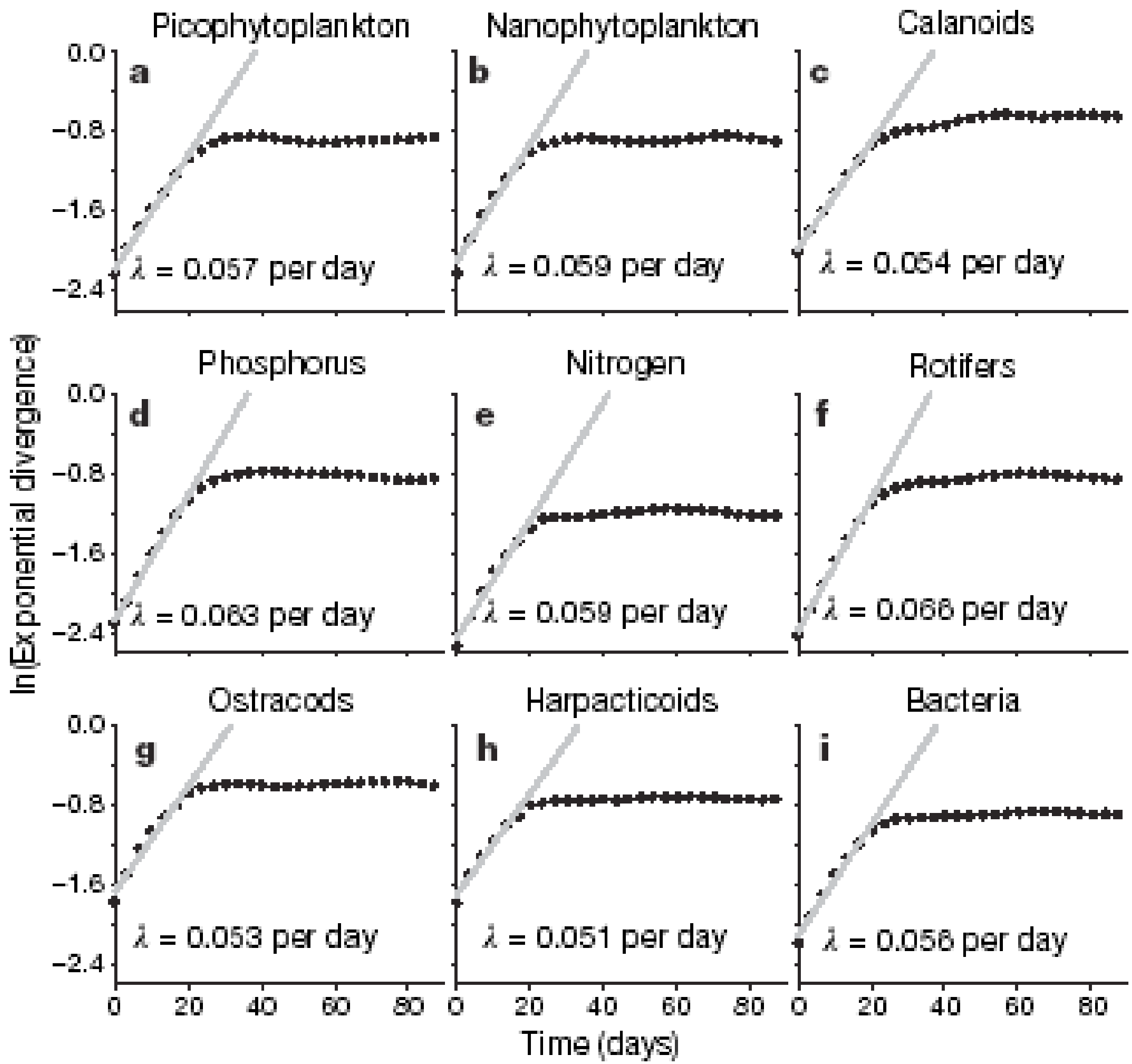


Figure 3 | Exponential divergence of the trajectories. The Lyapunov exponent (λ) is calculated as the initial slope of the ln-transformed

Learning outcomes

- Simple models can have complicated dynamics
- Even if you know exactly how things work, it doesn't mean you can predict them in the long term