演化
背後的動力學

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普通物理 (fall, 2013)

摘要

- 生物多樣性之謎
- 合作好？還是自私好呢？
- 細菌玩起剪刀石頭布？
- 結語

生物多様性

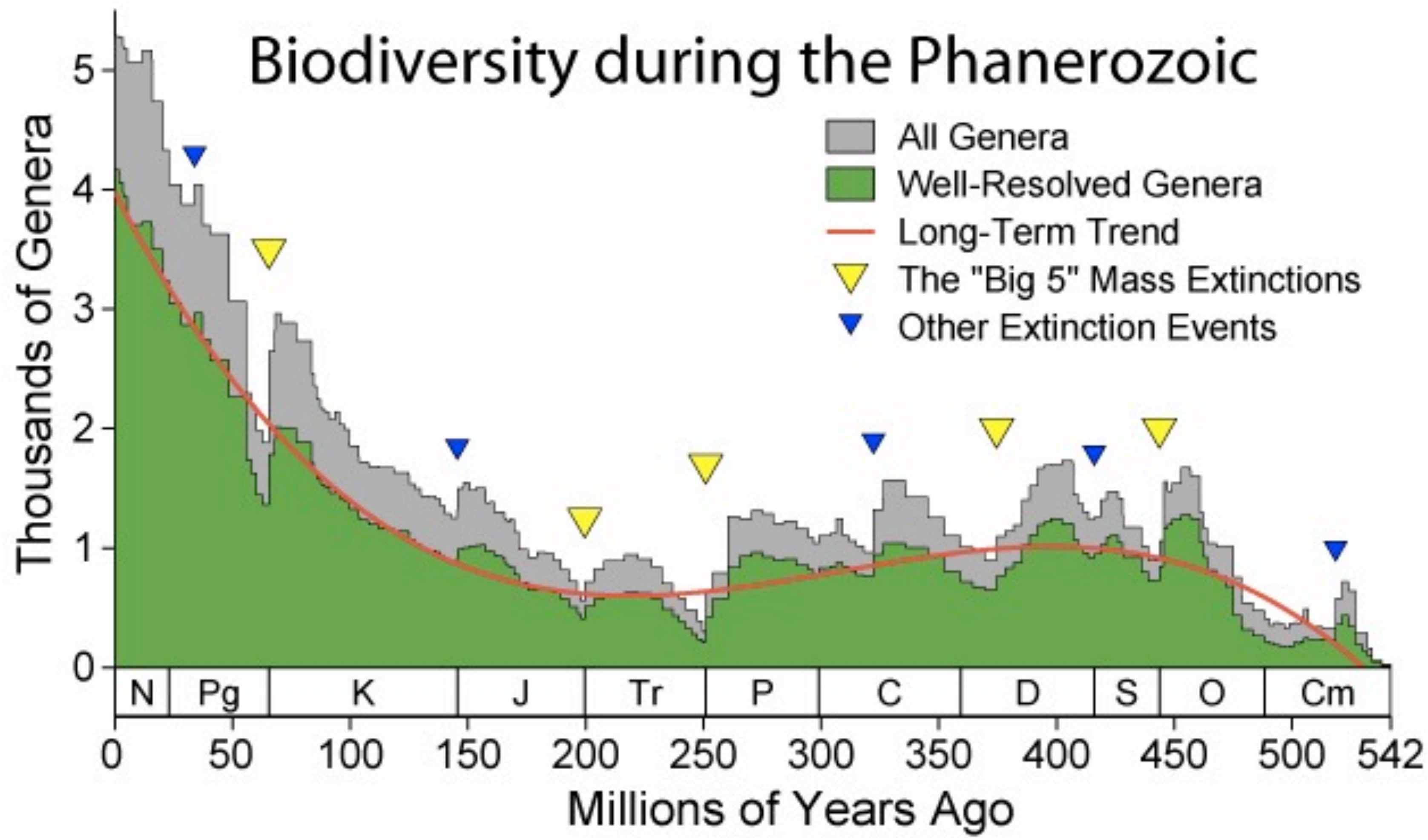
Biodiversity

多采多姿的生態

達爾文說物競天擇，適者生存。

那生態圈的生物多樣性是打那兒來的？

生物多樣性的歷史

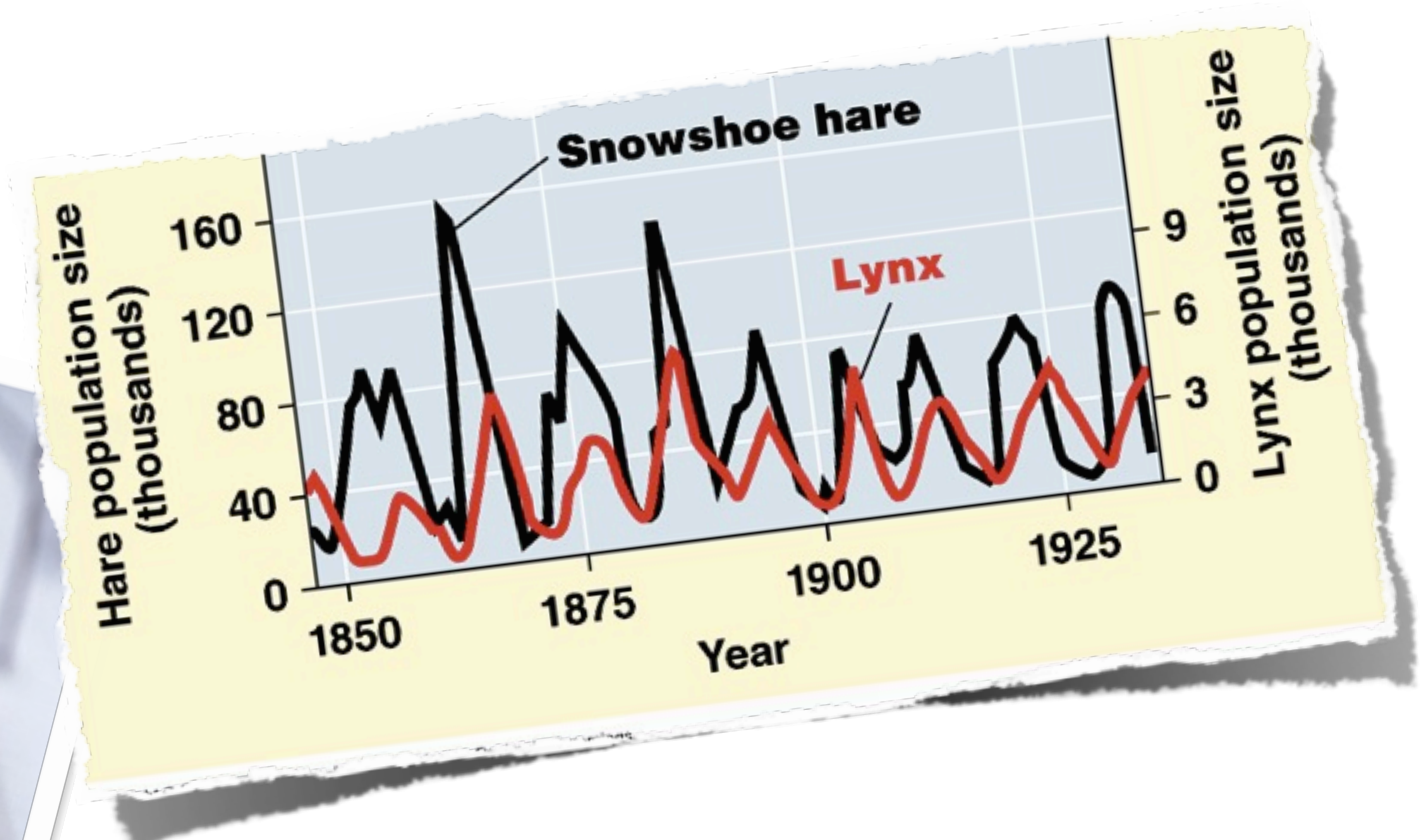


自寒武紀大爆發，物種大量出現。
但地球上的物種大滅絕，又為何發生？

雪兔與野貓

北加拿大的雪兔吃草，是素食主義的；
而野貓則是吃肉的，主要以雪兔為食。

兔口與貓口的統計



北加拿大的雪兔與野貓數量，
以十年左右做週期震盪。

出生與死亡

一小段時間後，族群數量改變了 $\Delta X \equiv X(t+\Delta t) - X(t)$

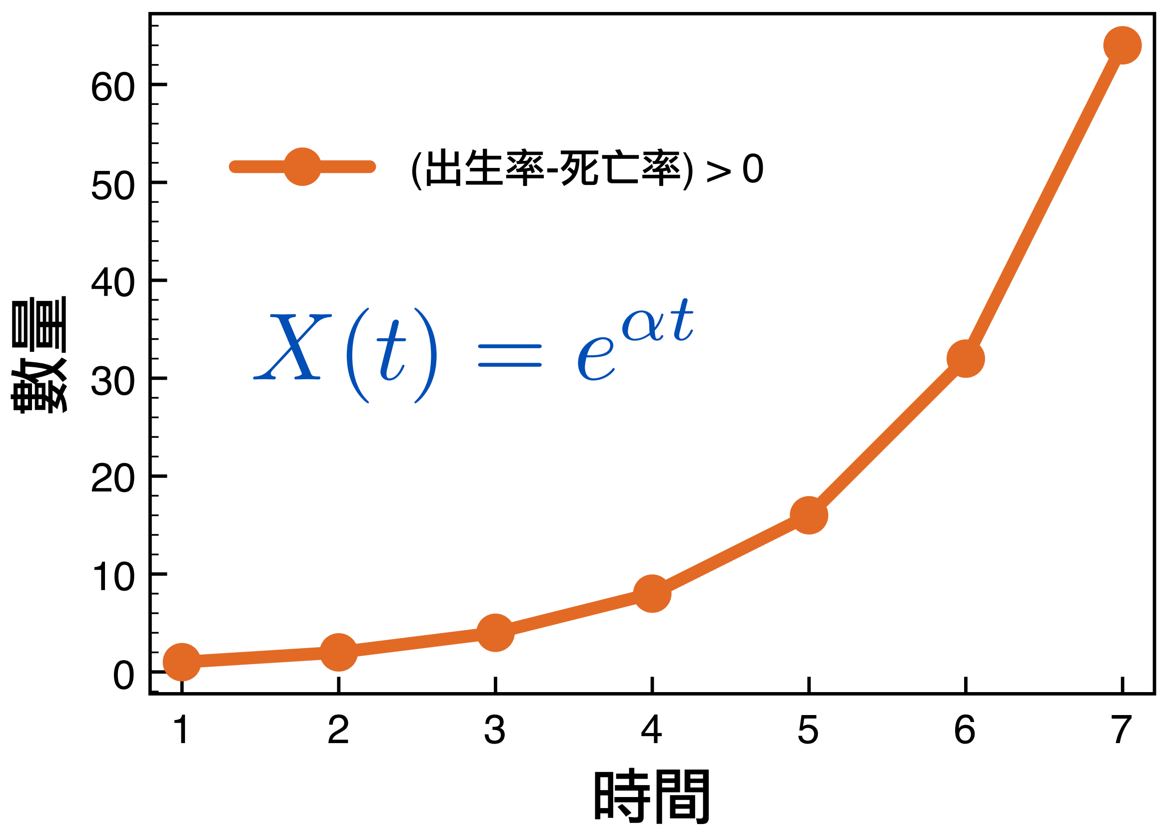
出生的數量： $Xb\Delta t$

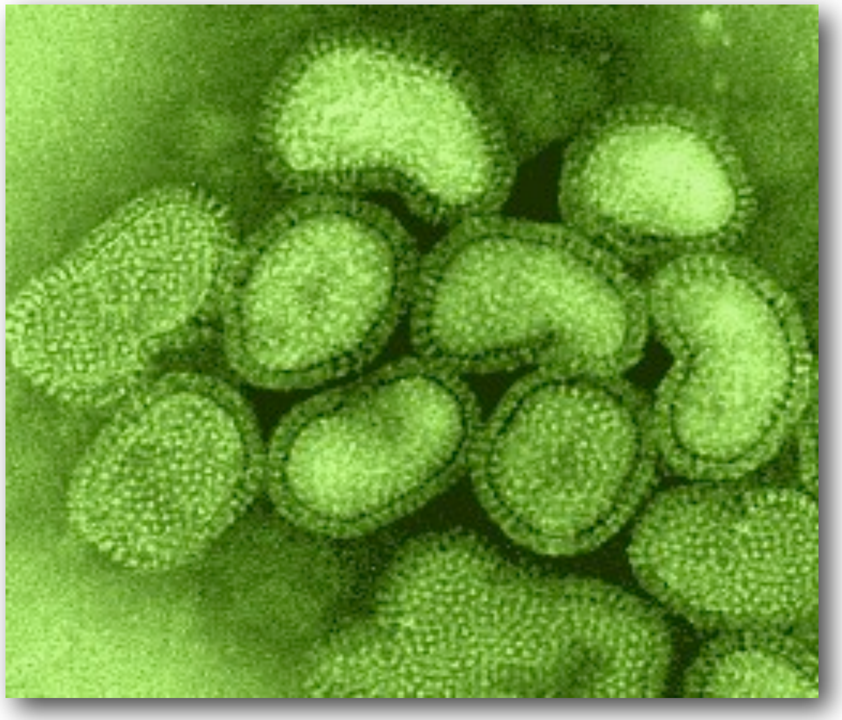
死亡的數量： $-Xd\Delta t$

適應力即為
出生率減死亡率

$$\boxed{\frac{\Delta X}{\Delta t} = (b-d)X}$$

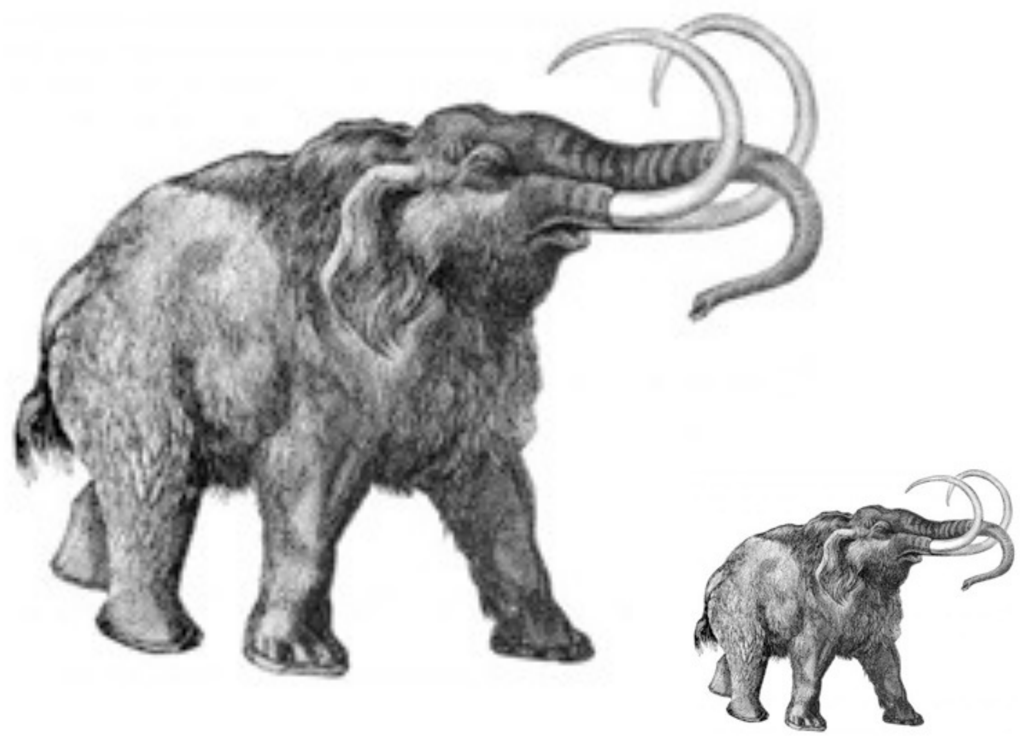
生生不息

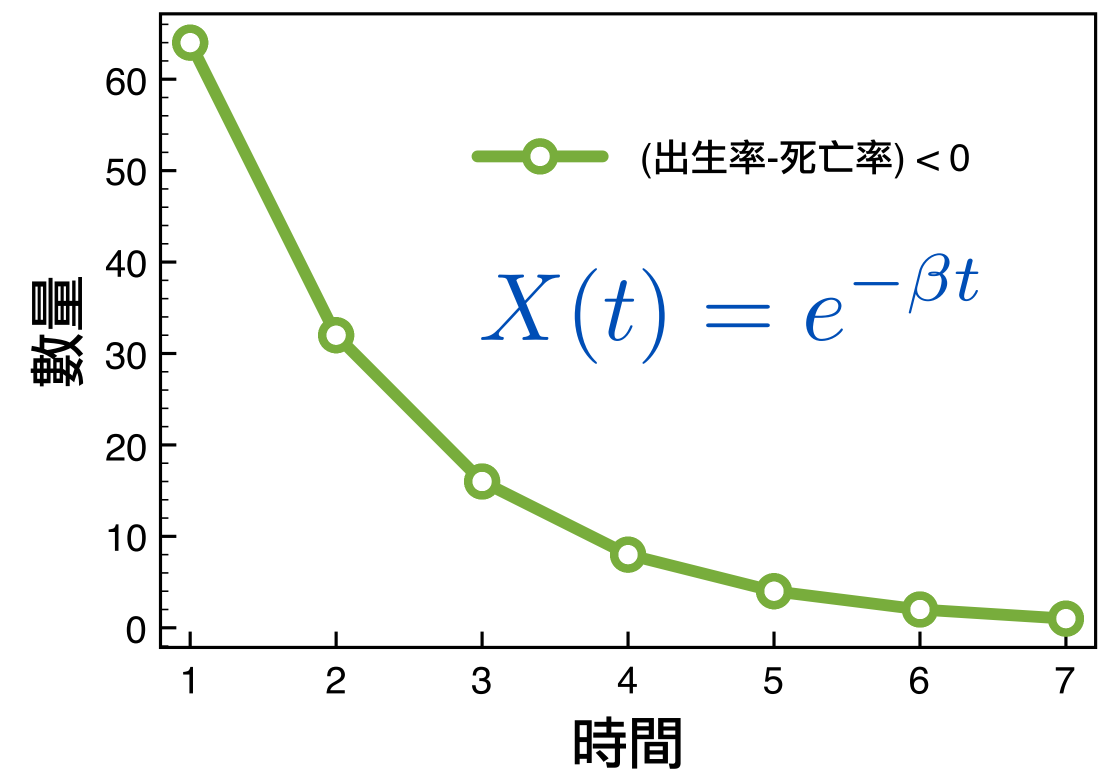




若出生率大於死亡率，族群數量呈指數增長。

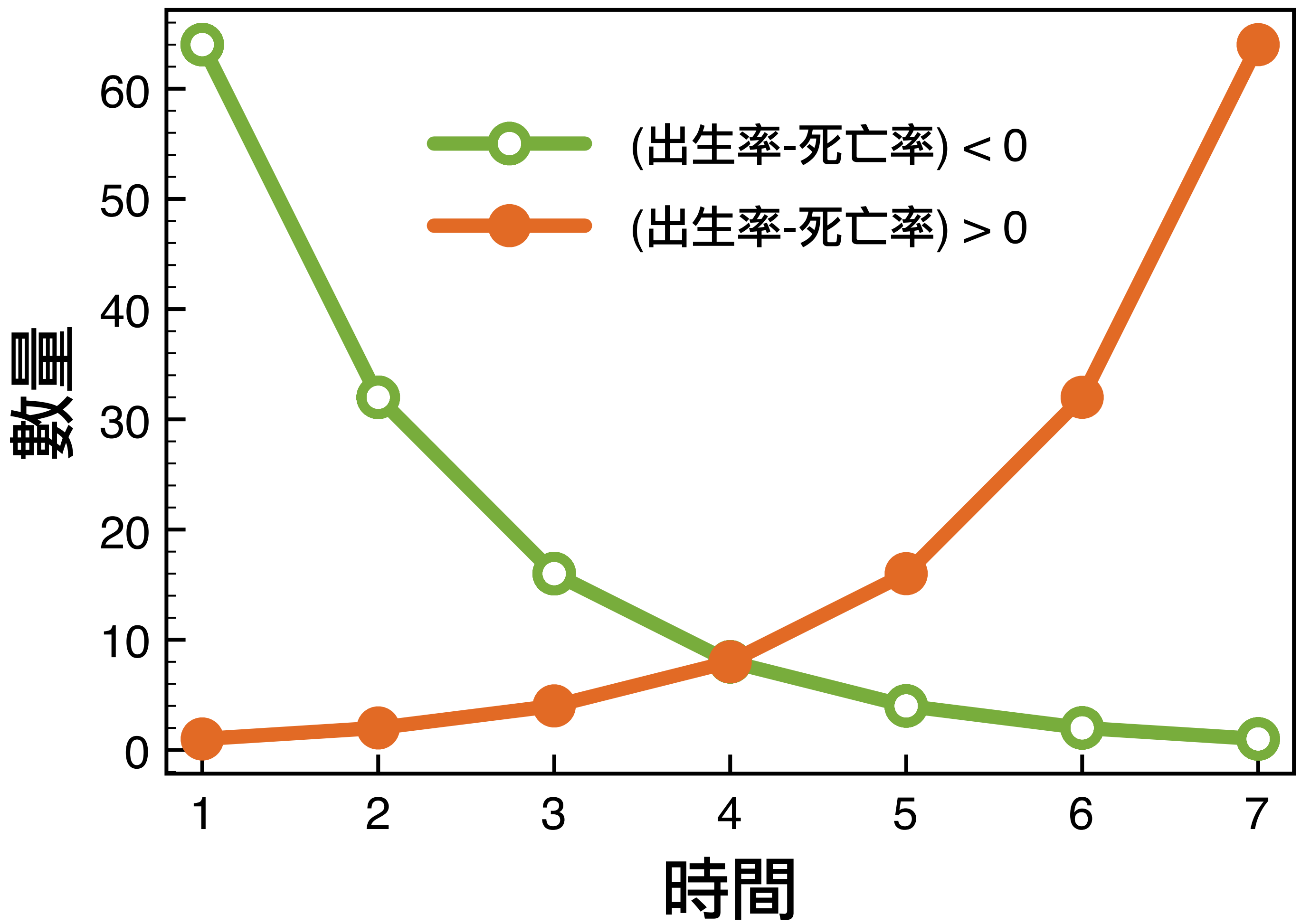
逐漸滅絕





若出生率小於死亡率，族群數量呈指數減少。

指數性的不穩定

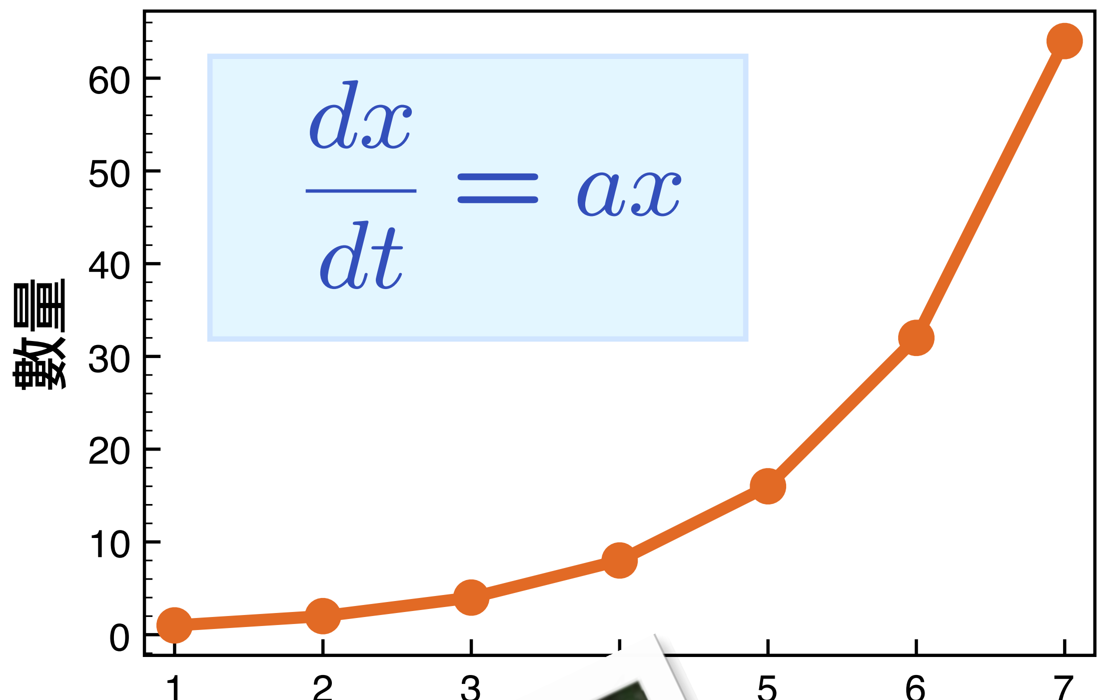


暴增…

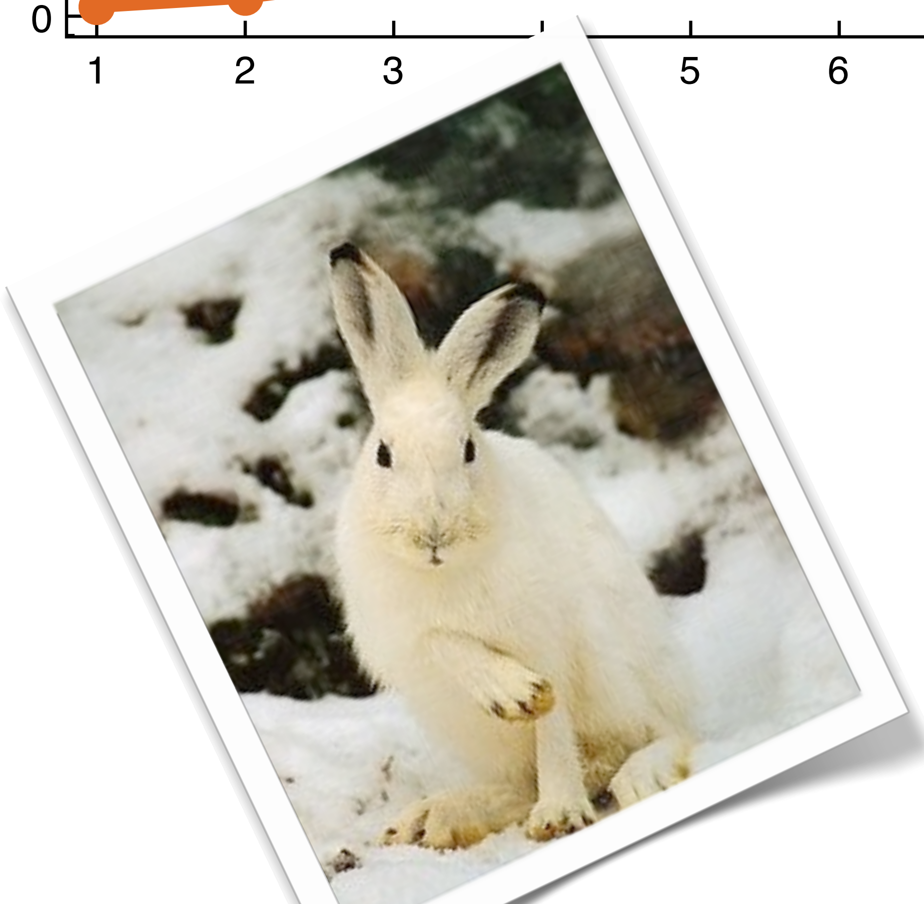
滅絕…

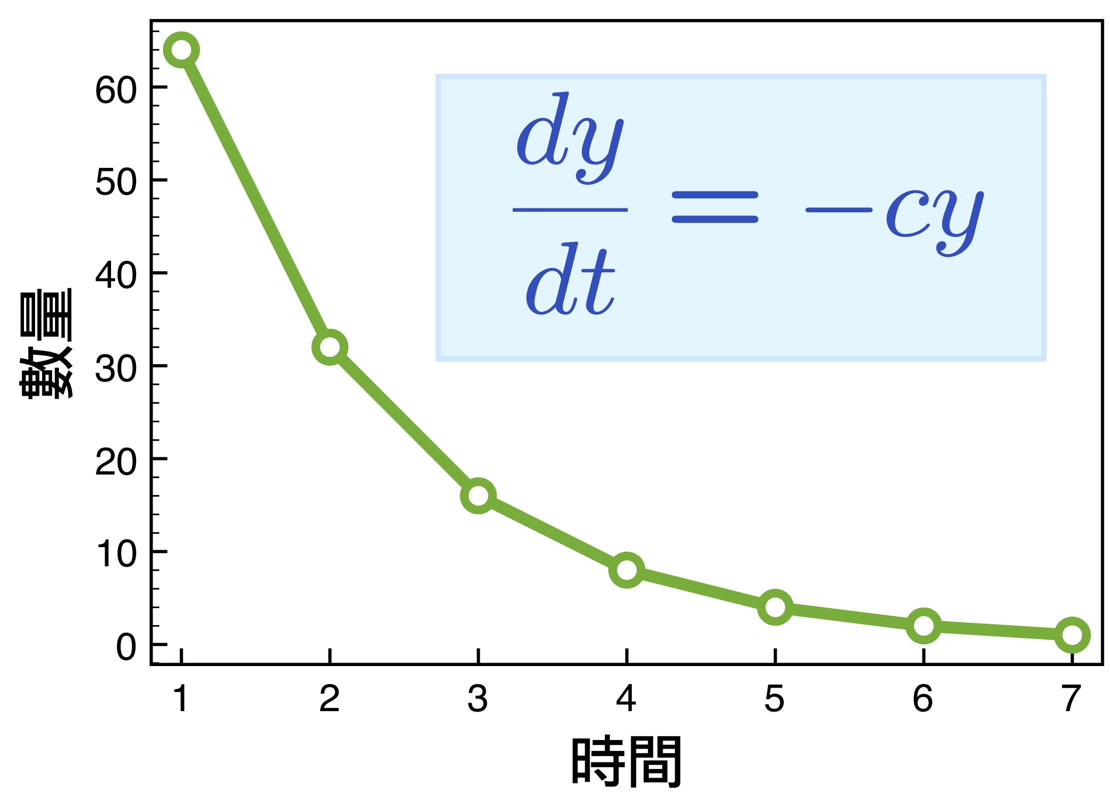
暴增？滅絕？沒有其他的選擇嗎？

狩獵者遇到獵物前



$$\frac{dx}{dt} = ax$$
數量
0
10
20
30
40
50
60
1
2
3
5
6
7



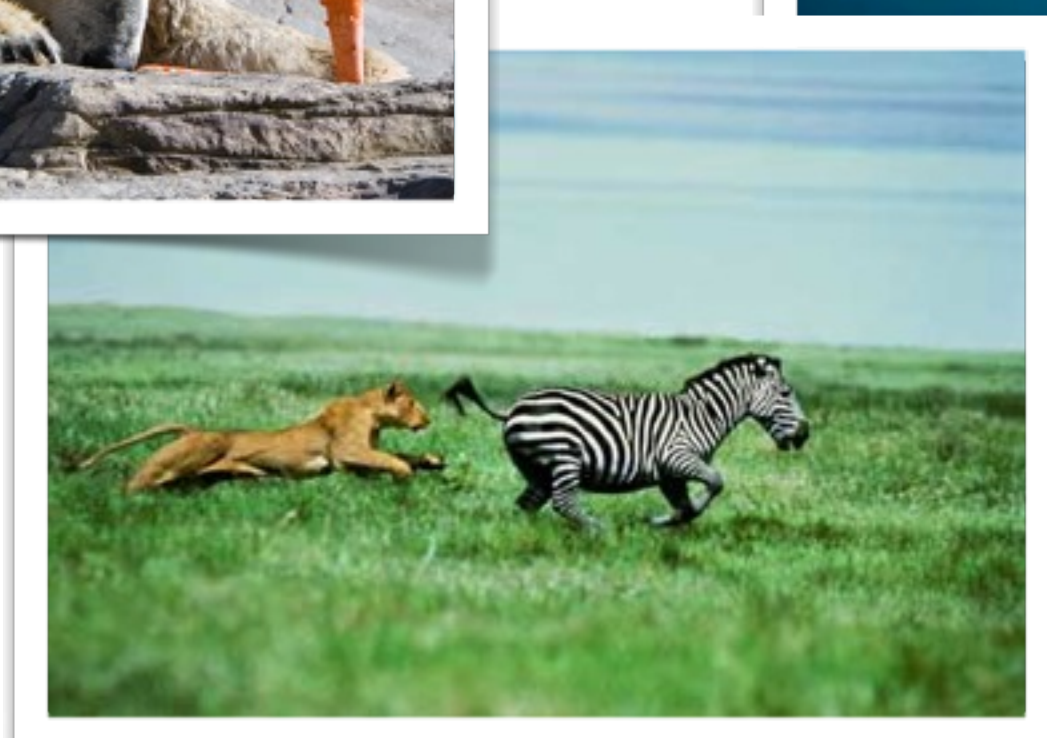


$$\frac{dy}{dt} = -cy$$
數量
0
10
20
30
40
50
60
1
2
3
4
5
6
7
時間

弱肉強食

強壯的捕捉弱小的，攸關生死的追逐。

弱肉強食的結果



生生不息的
平衡？

Lotka-Volterra model

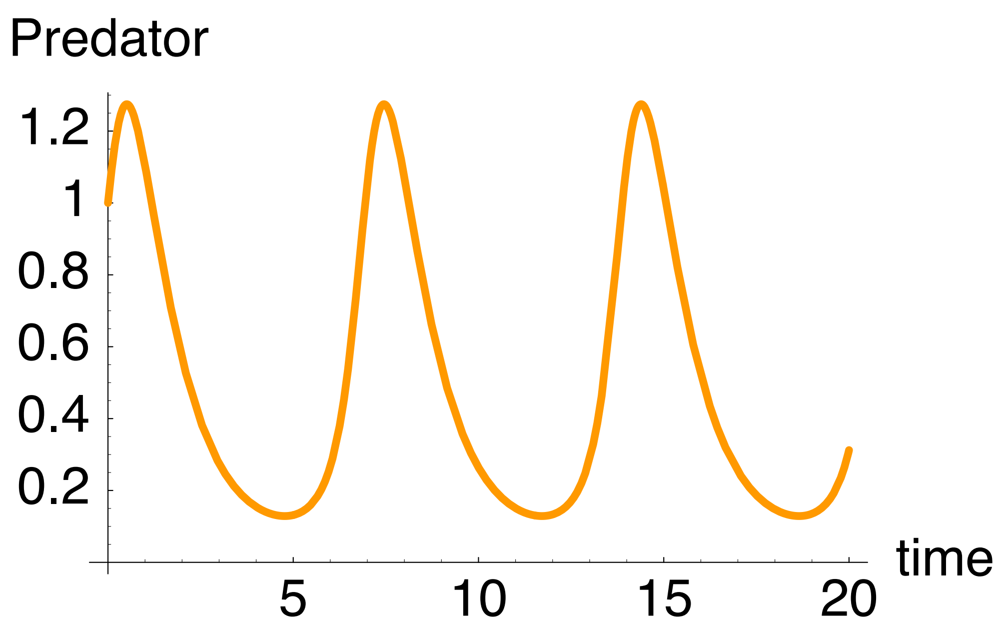
The **Lotka-Volterra equations**, also known as the *predator-prey equations*, are a pair of first order, non-linear, differential equations frequently used to describe the dynamics of biological systems in which two species interact, one a predator and one its prey. They were proposed independently by Alfred J. Lotka in 1925 and Vito Volterra in 1926.

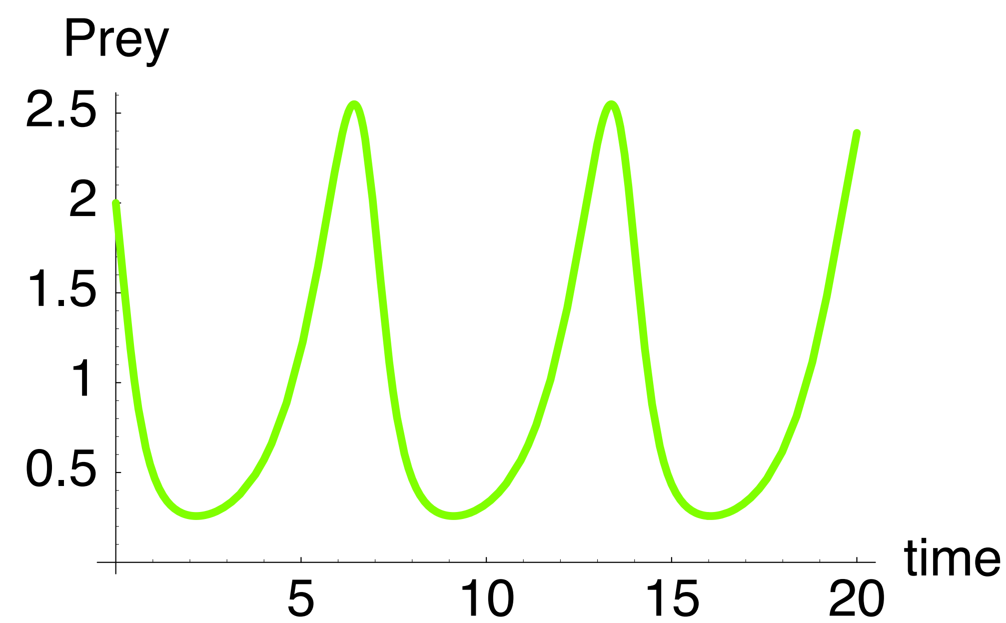
$$\begin{aligned} \frac{dx}{dt} &= (a - by)x \\ \frac{dy}{dt} &= (-c + dx)y \end{aligned}$$

where

- *y* is the number of some predator (for example, wolves);
- *x* is the number of its prey (for example, rabbits);
- *dy/dt* and *dx/dt* represents the growth of the two populations against time;
- *t* represents the time; and
- *a*, *b*, *c* and *d* are parameters representing the interaction of the two species.

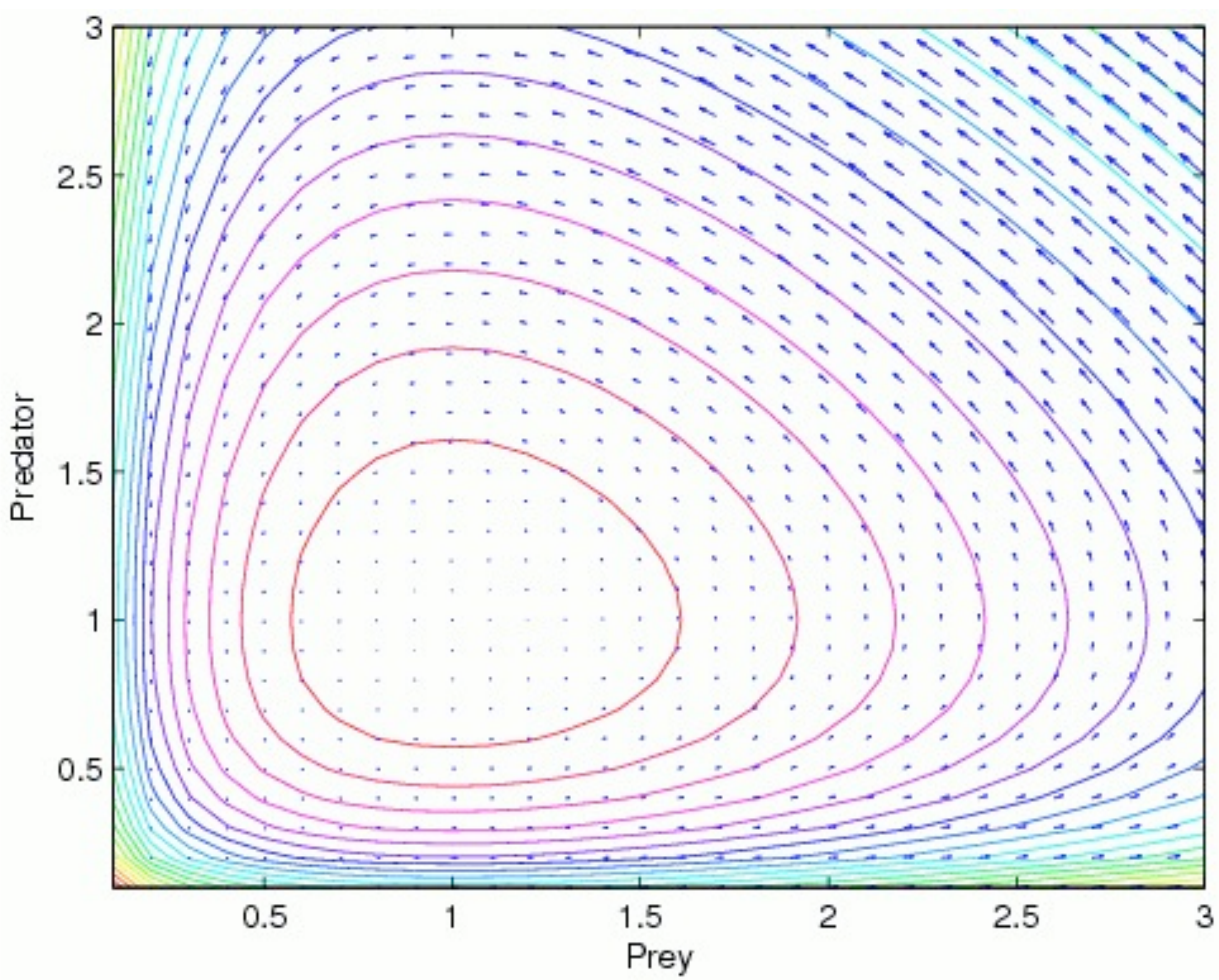
貓口與兔口的震盪





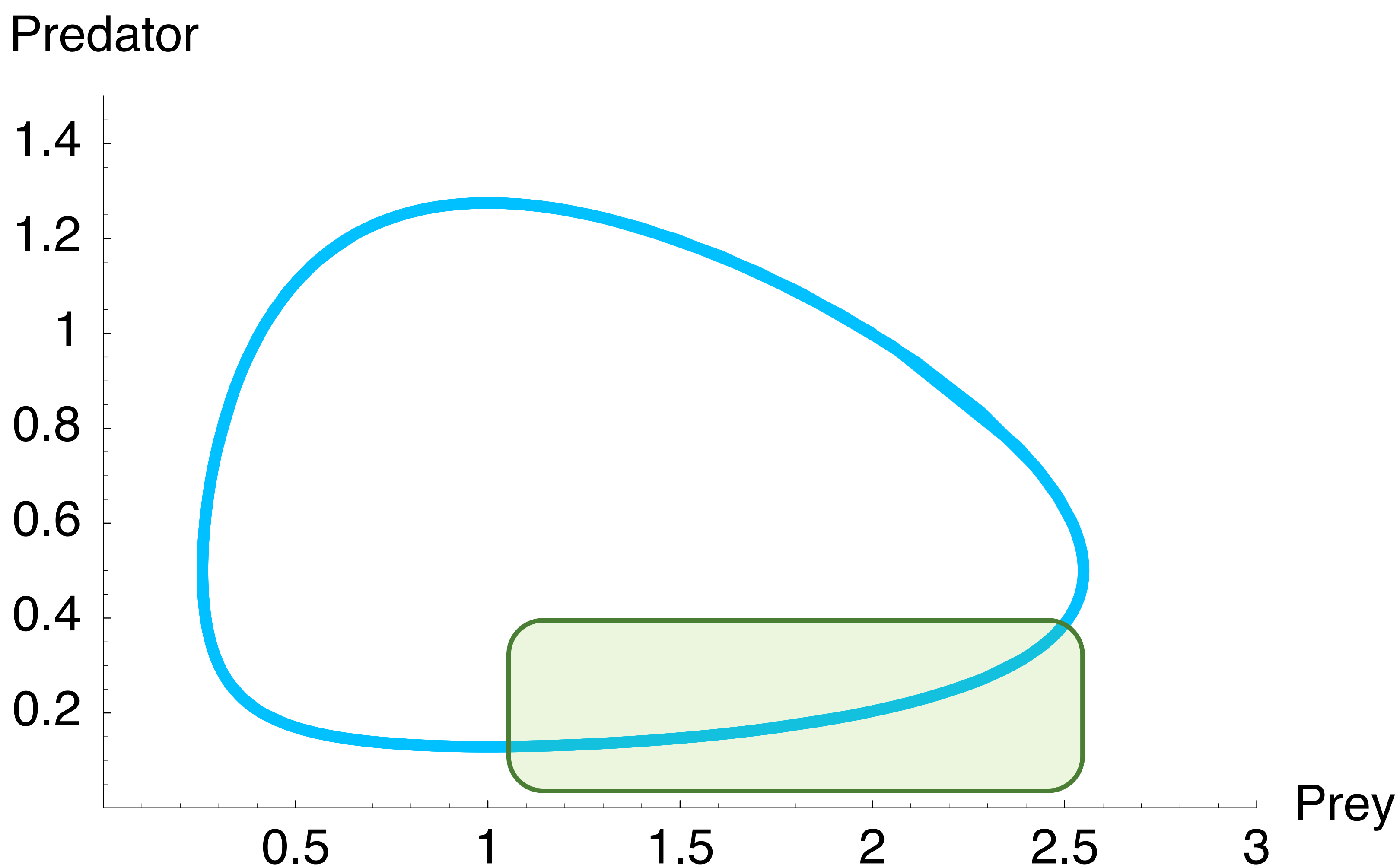
雪兔與野貓同時存在，弱肉強食的演化機制下，貓口與兔口同時出現震盪。

生命的迴圈



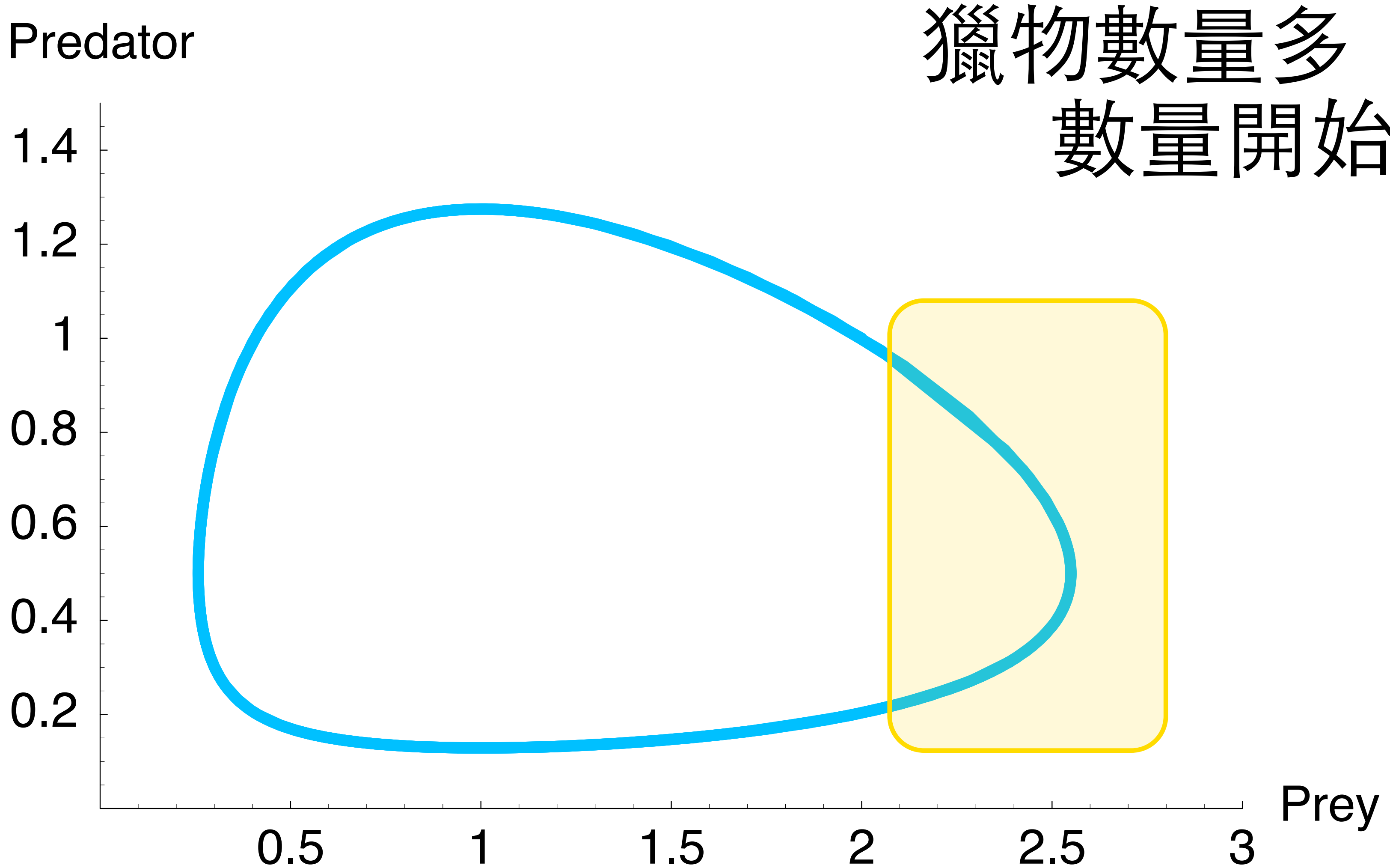
將貓口與兔口畫在一起，結果十分有趣，出現一個個週期性的圈圈。

生態系的動平衡



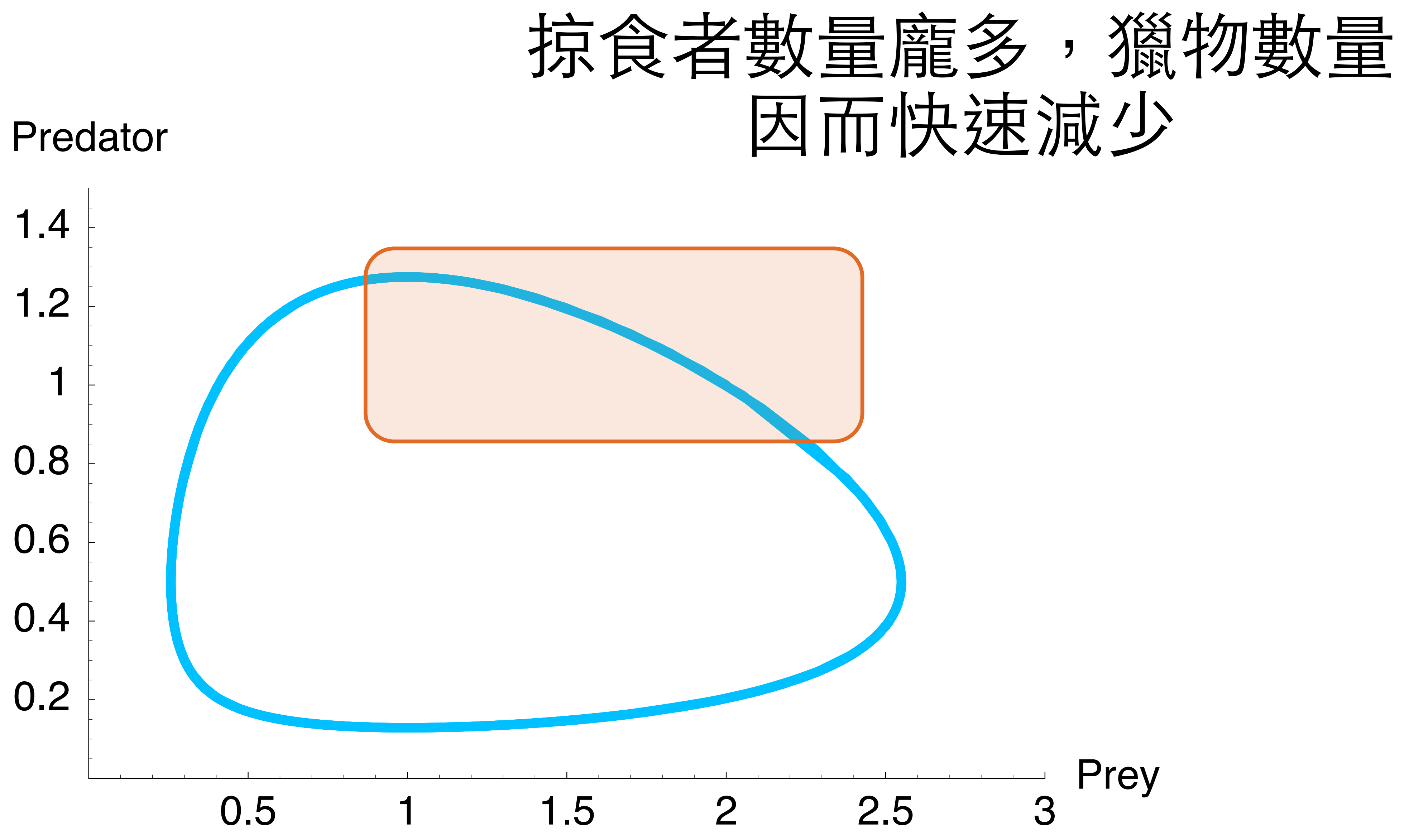
掠食者數量稀少，獵物大量繁殖

生態系的動平衡



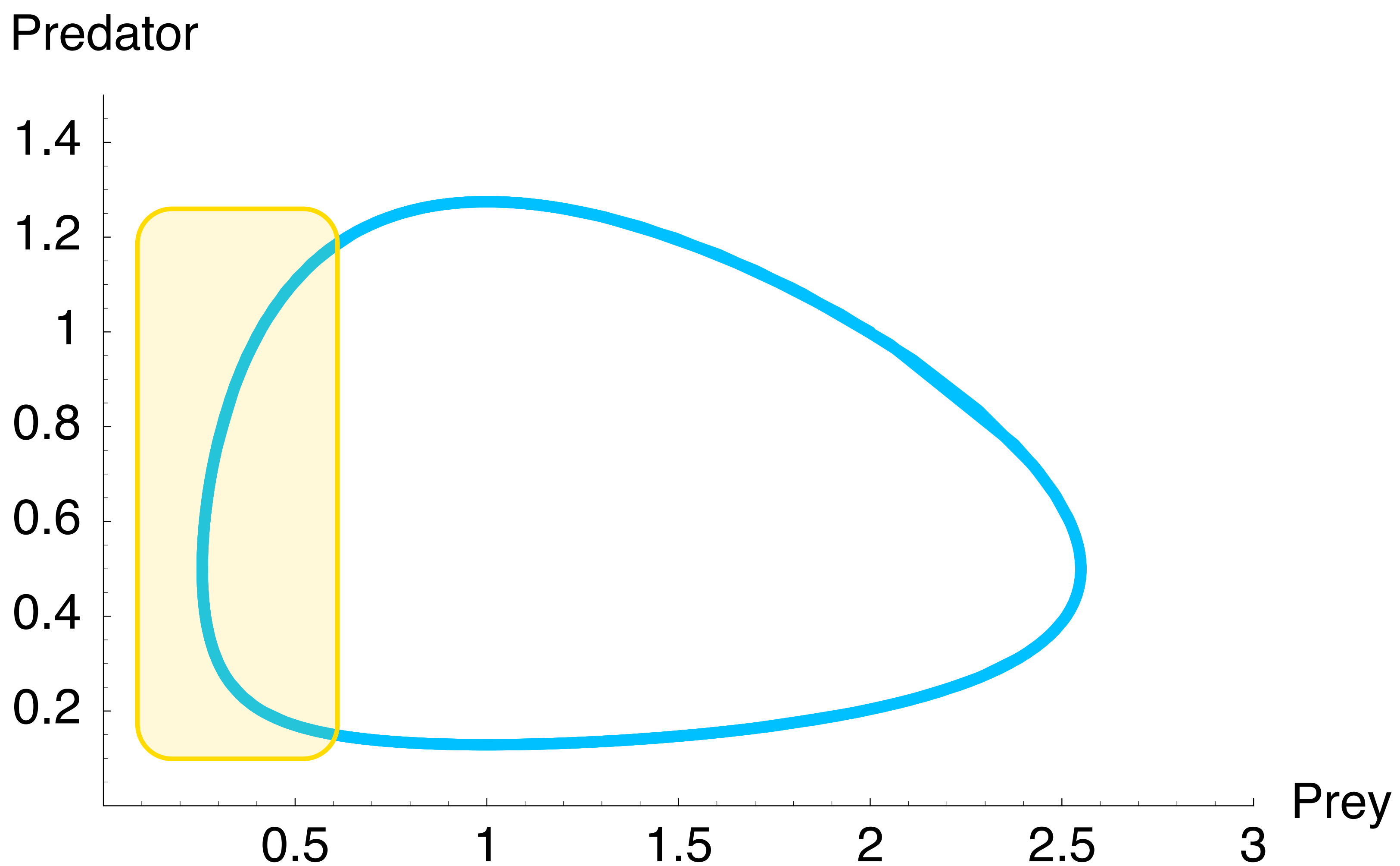
獵物數量多，掠食者
數量開始增加

生態系的動平衡



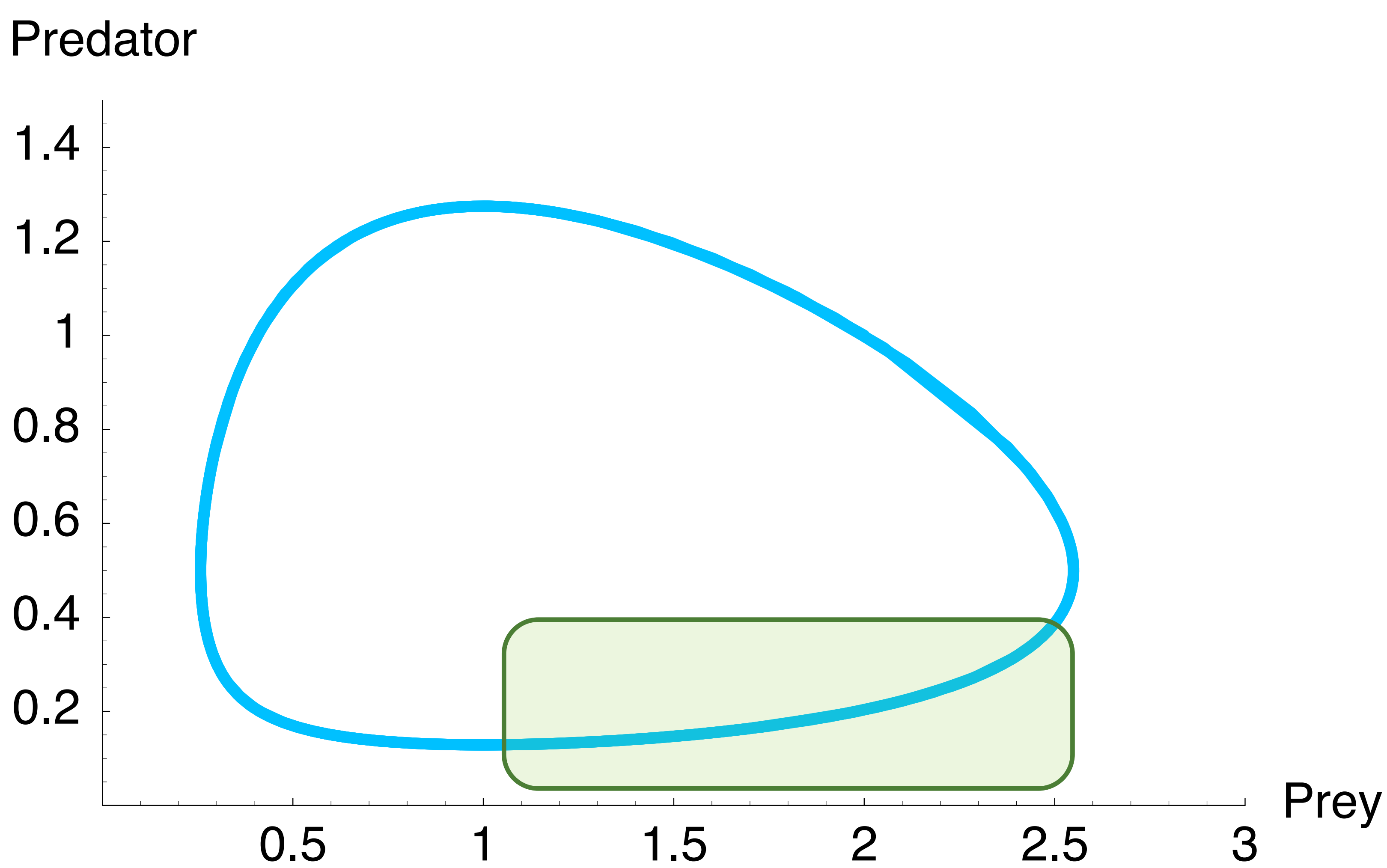
掠食者數量龐多，獵物數量
因而快速減少
Predator
1.4
1.2
1
0.8
0.6
0.4
0.2
0.5
1
1.5
2
2.5
3
Prey

生態系的動平衡



因獵物稀少，掠食者數量
開始下降

生態系的動平衡



掠食者數量稀少，獵物大量繁殖

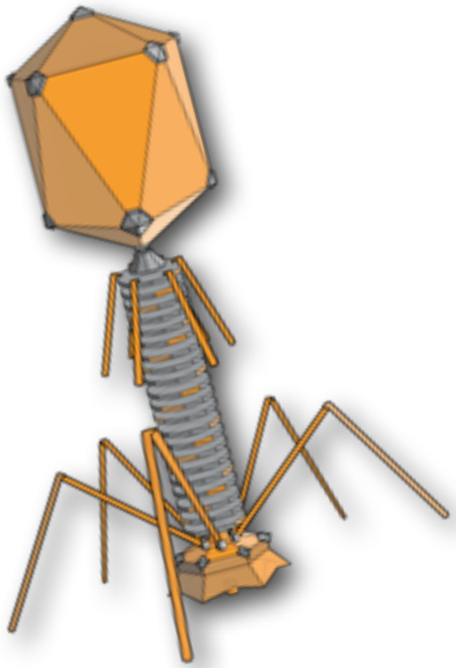
生物多樣性之謎

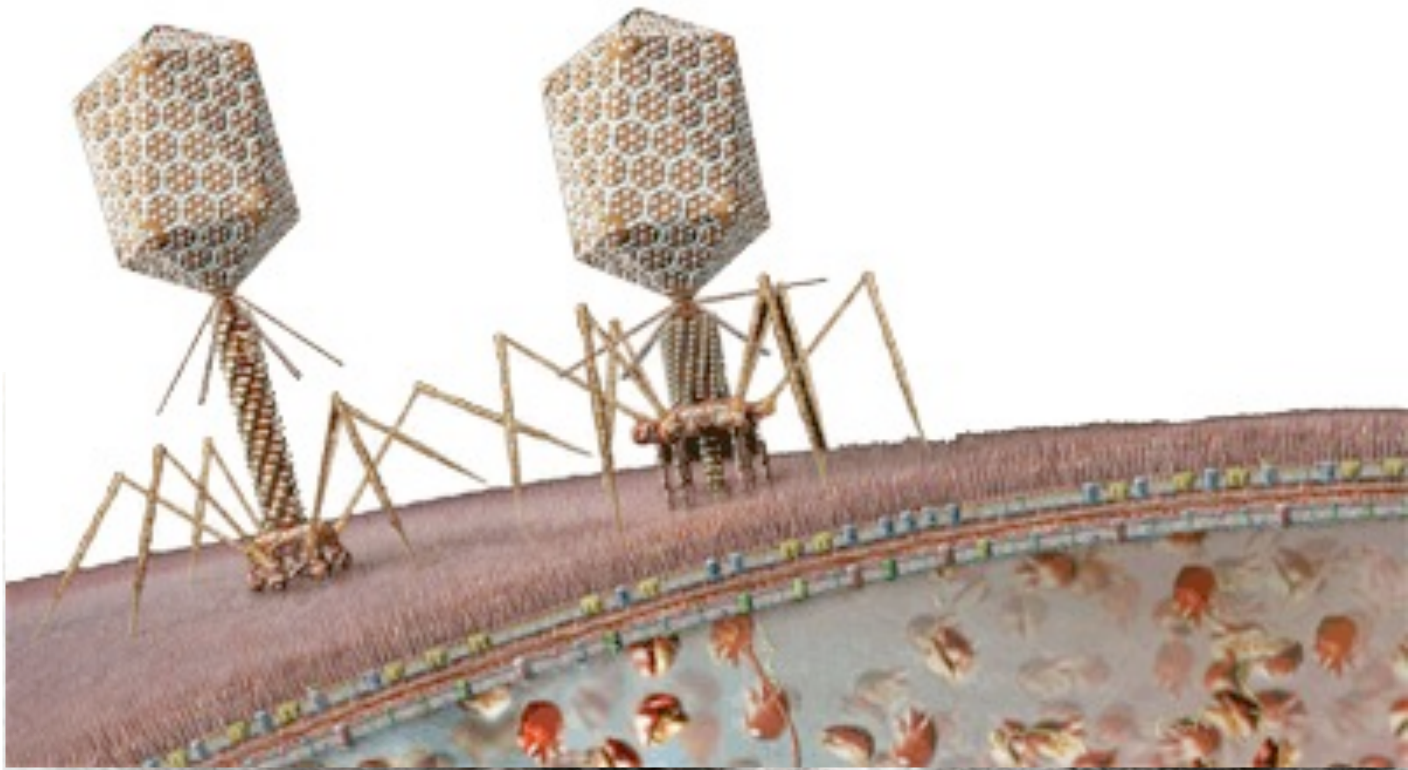
物種間的競爭形成動態平衡，使生態圈的物種得以生生不息。

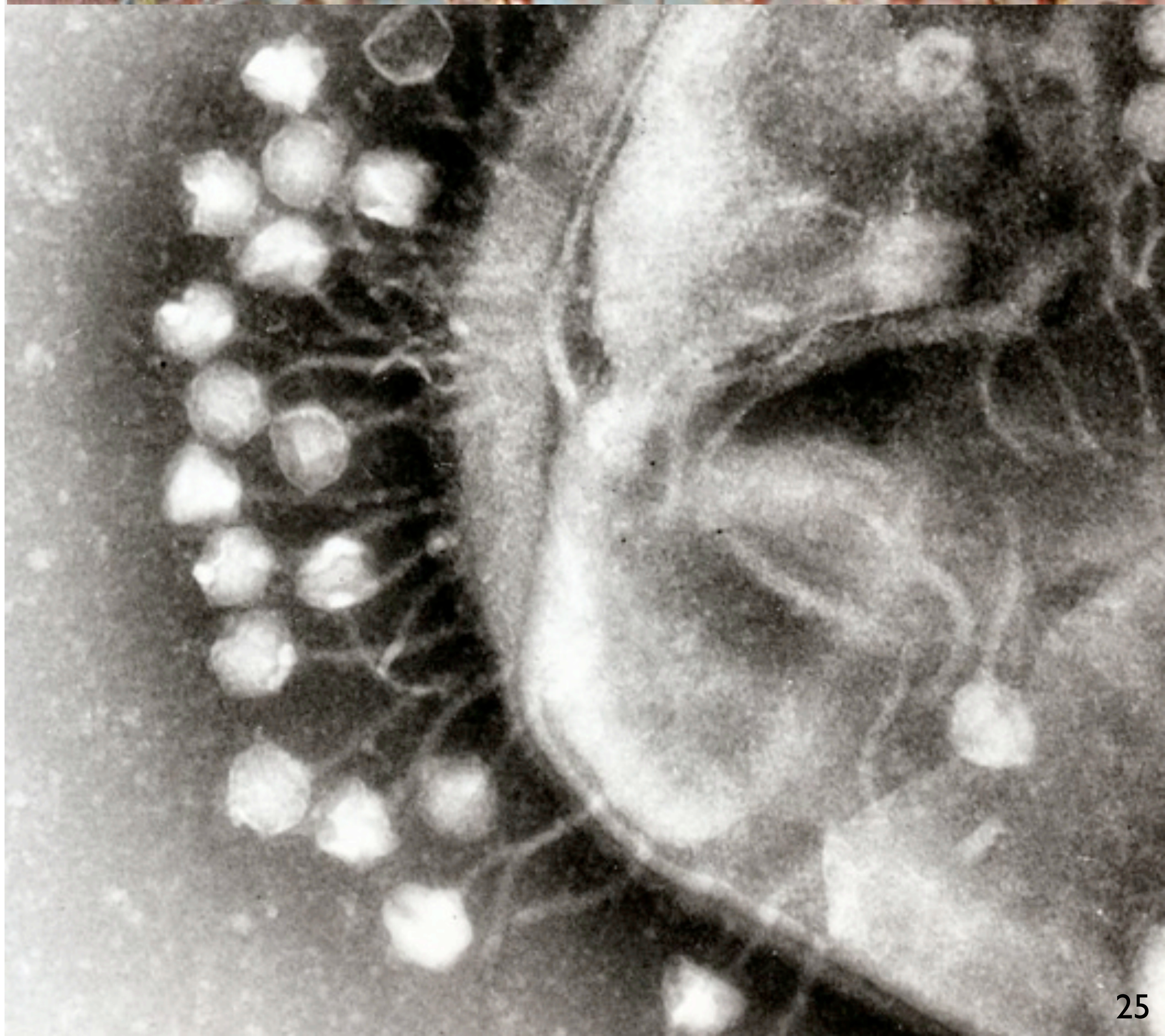
這樣微妙的動態平衡，正解釋了自然界處處可見的生物多樣性。

噬菌體的戰爭

噬菌體

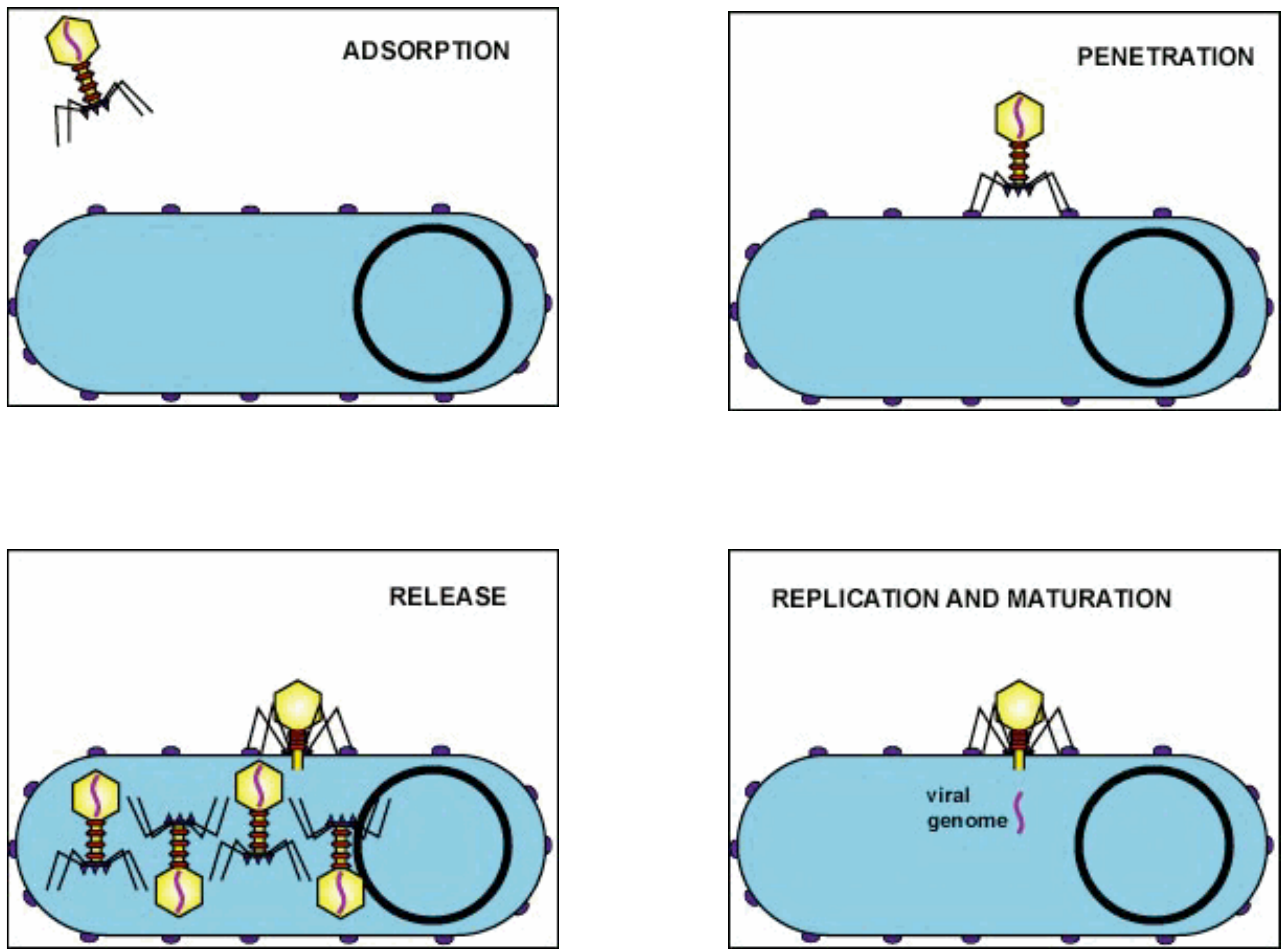






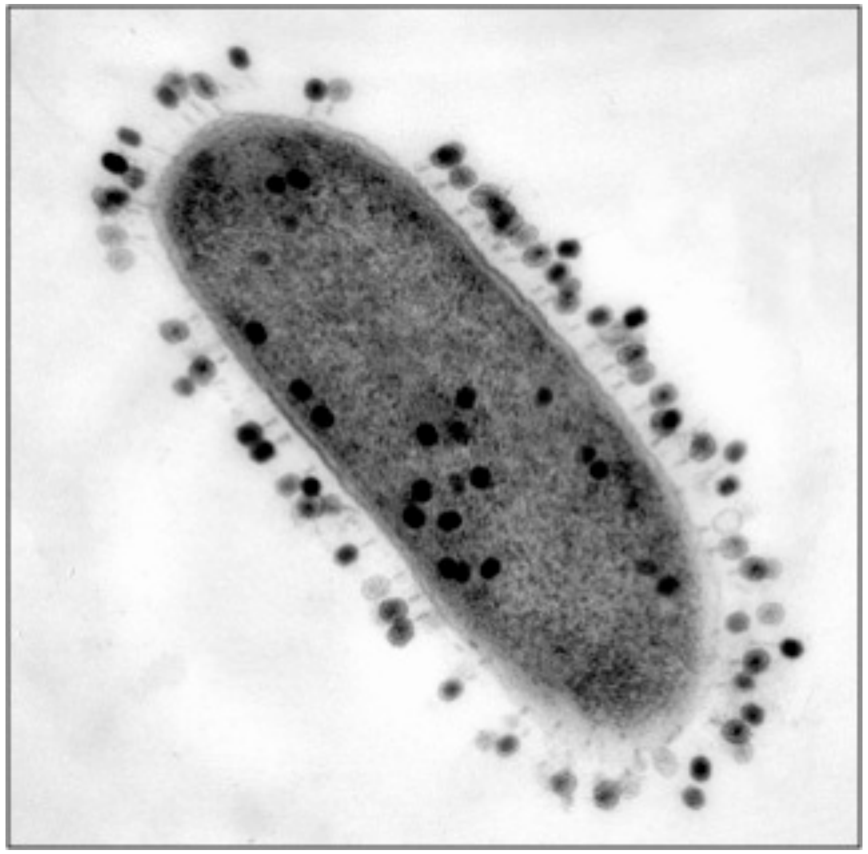
顧名思義，噬菌體是一種專吃細菌的病毒。

異形入侵


ADSORPTION
PENETRATION
RELEASE
REPLICATION AND MATURATION
viral
genome

合作 v.s. 自私

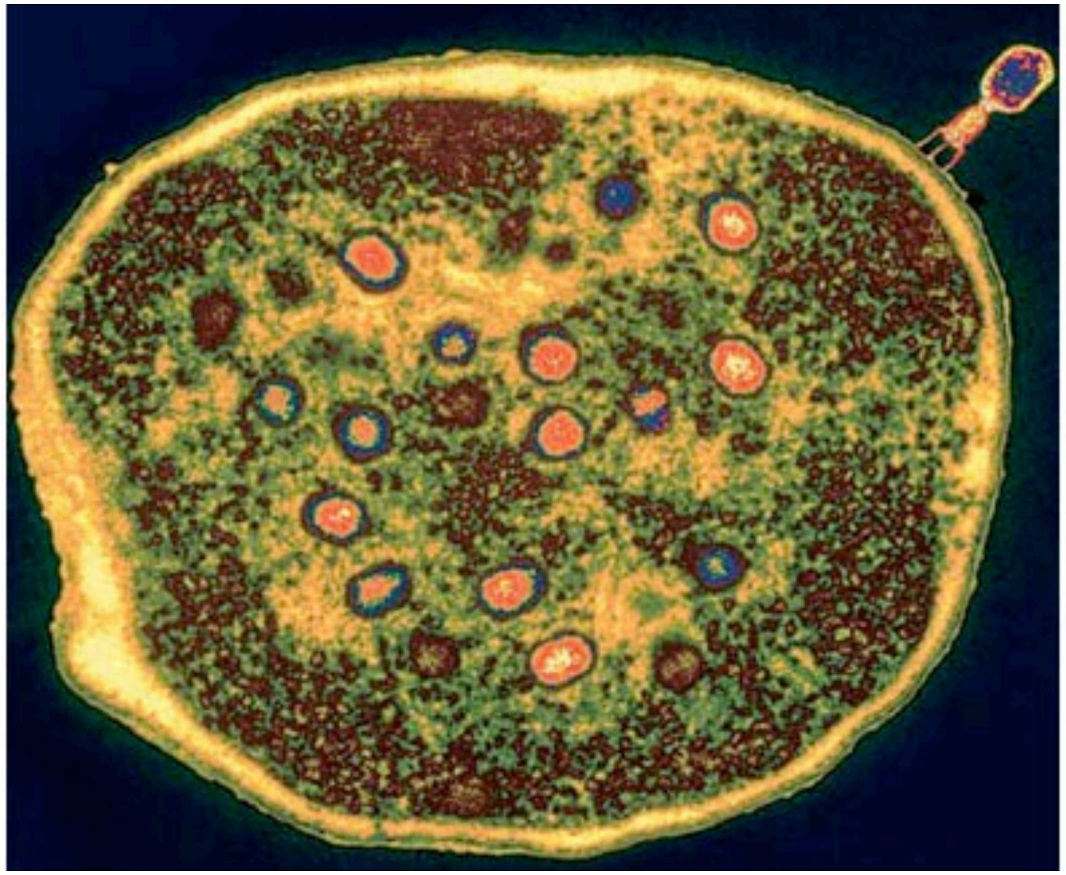
合作者：彼此幫助，適應力強，一般稱為好人或是濫好人。

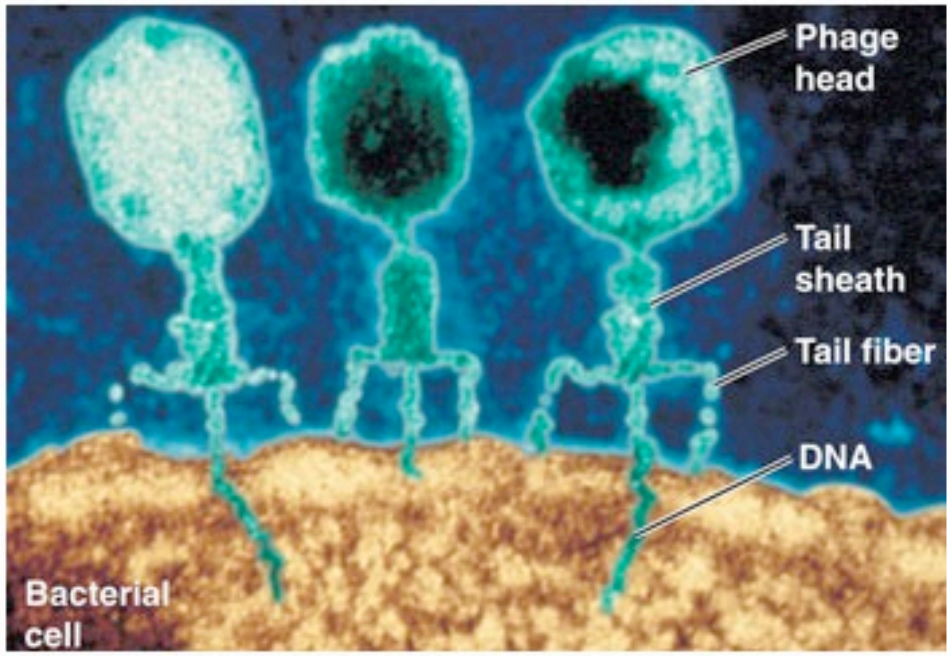


自私者：勾心鬥角，自私自利，一般稱為壞蛋或是混蛋。

自私的活下來？

Nature **398**, 441 (1999)



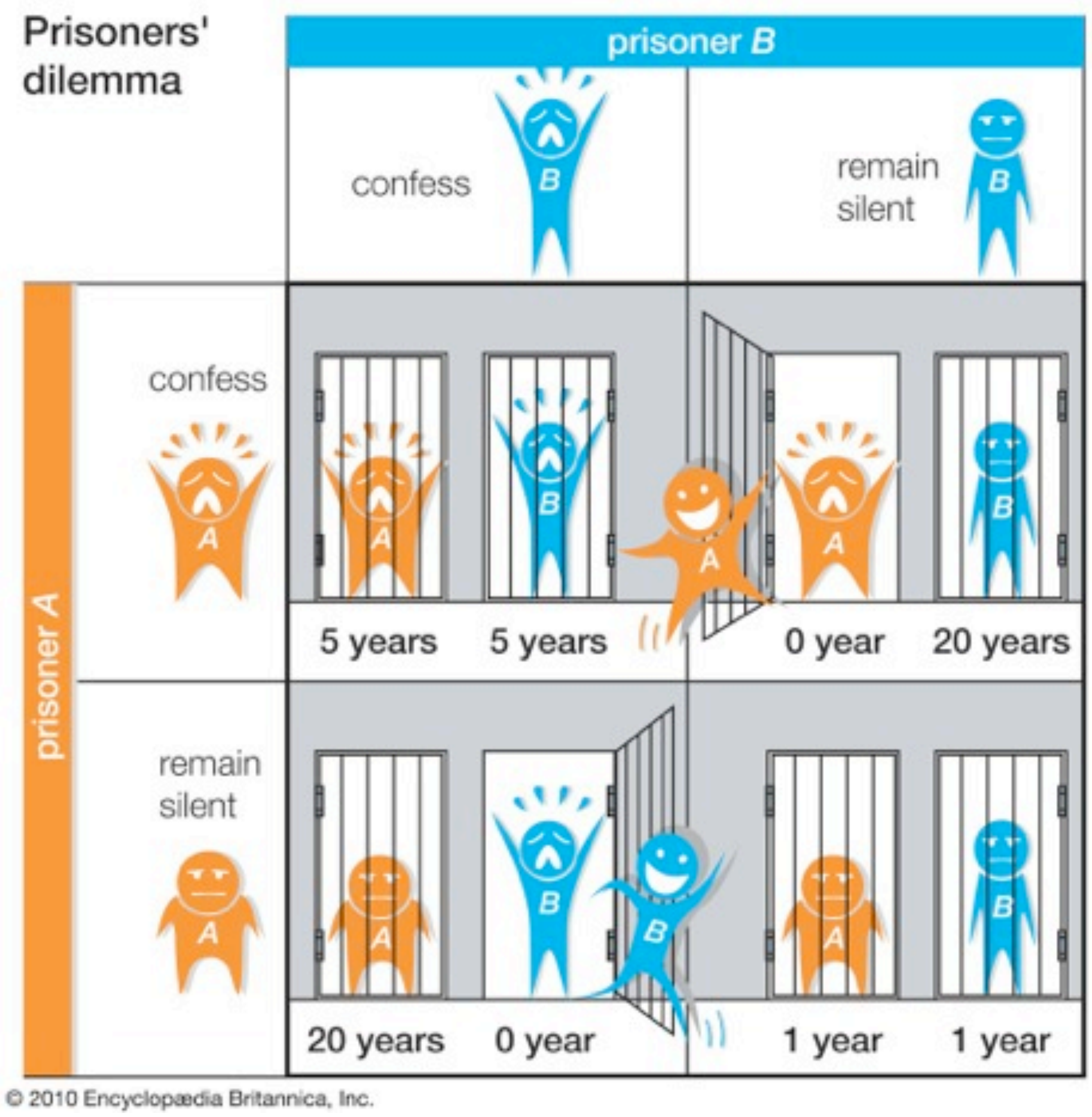


美國馬里蘭大學學者發現，長得慢又很壞的自私型噬菌體大獲全勝！

犯人的困境

做壞事被抓時，是該合作？（打死不承認）
還是該自私一點？（出賣同夥）

合作？出賣？



天真的想法

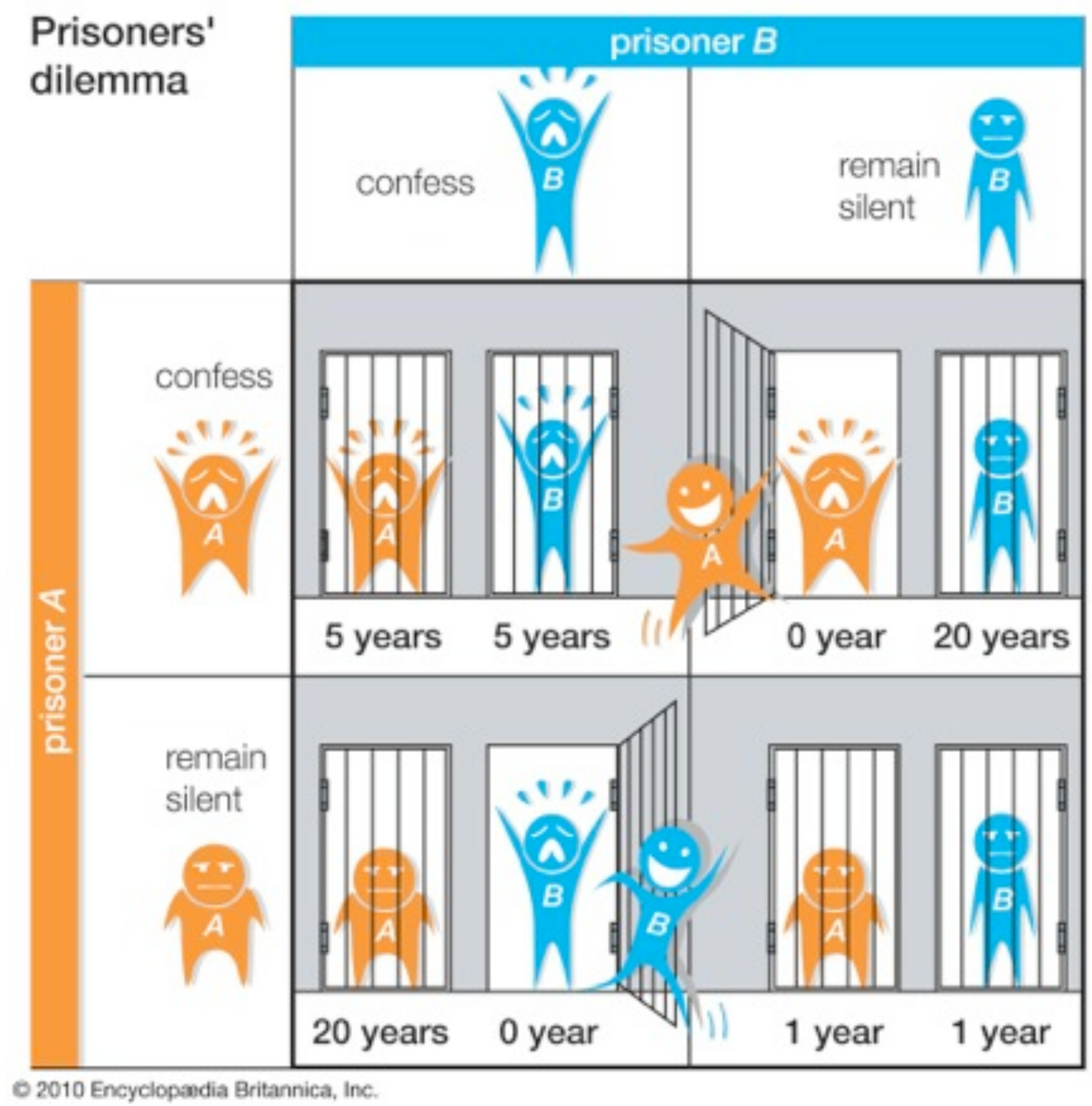
如果一起出賣對方而承認，就被關五年。如果一起合作來個矢口否認，那罪證不足，頂多被關一年。

出來混的，果真是要講義氣啊！

出賣才是理性的抉擇

理性的想法

如果對方出賣我而認罪，我應該也出賣他。如果對方合作而矢口否認，那更該出賣他。



哎啊，出賣對方才是王道！

無所不在的補習

補習，是大多數台灣小孩的共同回憶。多年的教育改革後，補習班為何還這麼多？

你小孩補習嗎？

	正常	惡補
正常	10	6
惡補	20	8

合作：如果大家都不補習，小孩子的適應力為10。

自私：如果大家都送小孩去補習，適應力反而降為 8。

競爭力估算

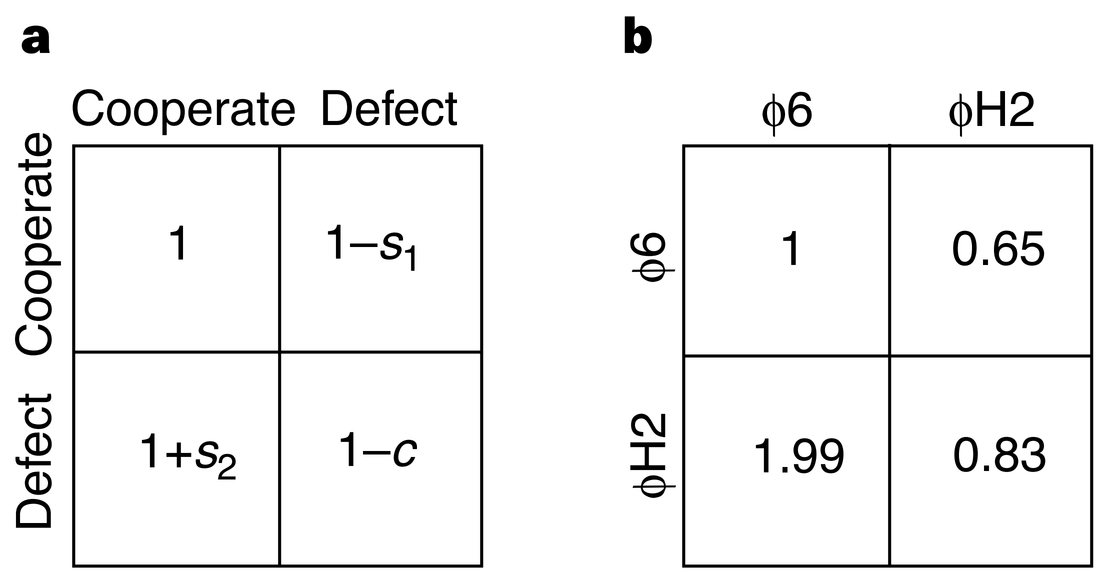
	正常	惡補
正常	10	6
惡補	20	8

假設台灣社會合作型家長比例是 x。

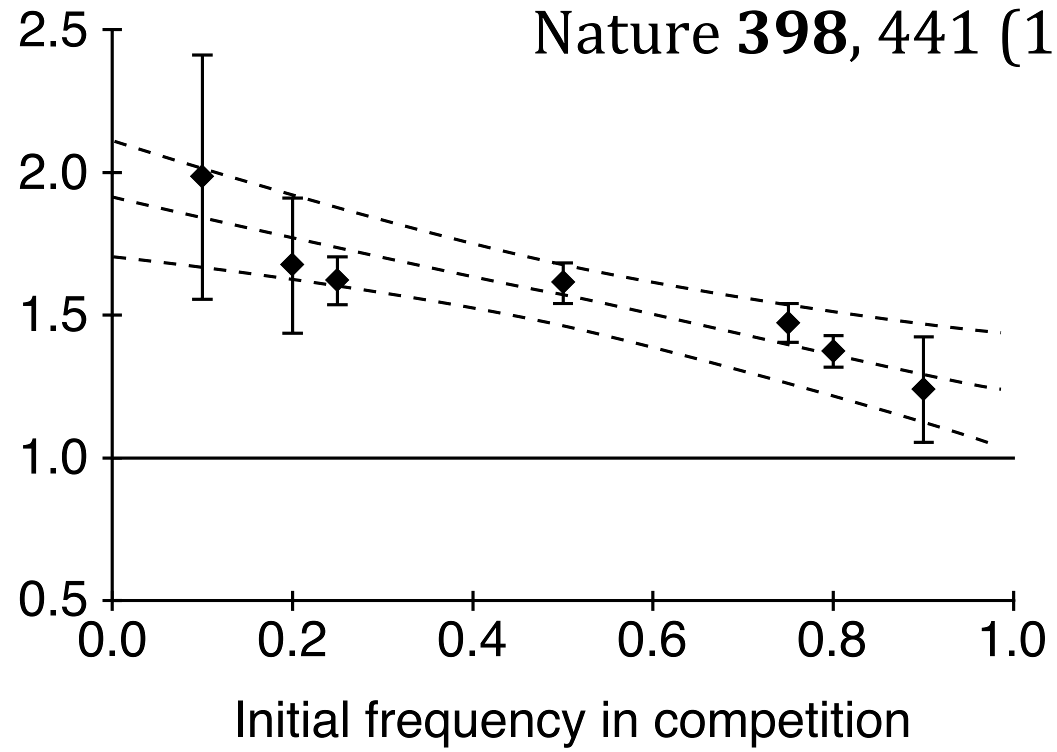
$$F_C = 10x + 6(1-x) = 6 + 4x$$

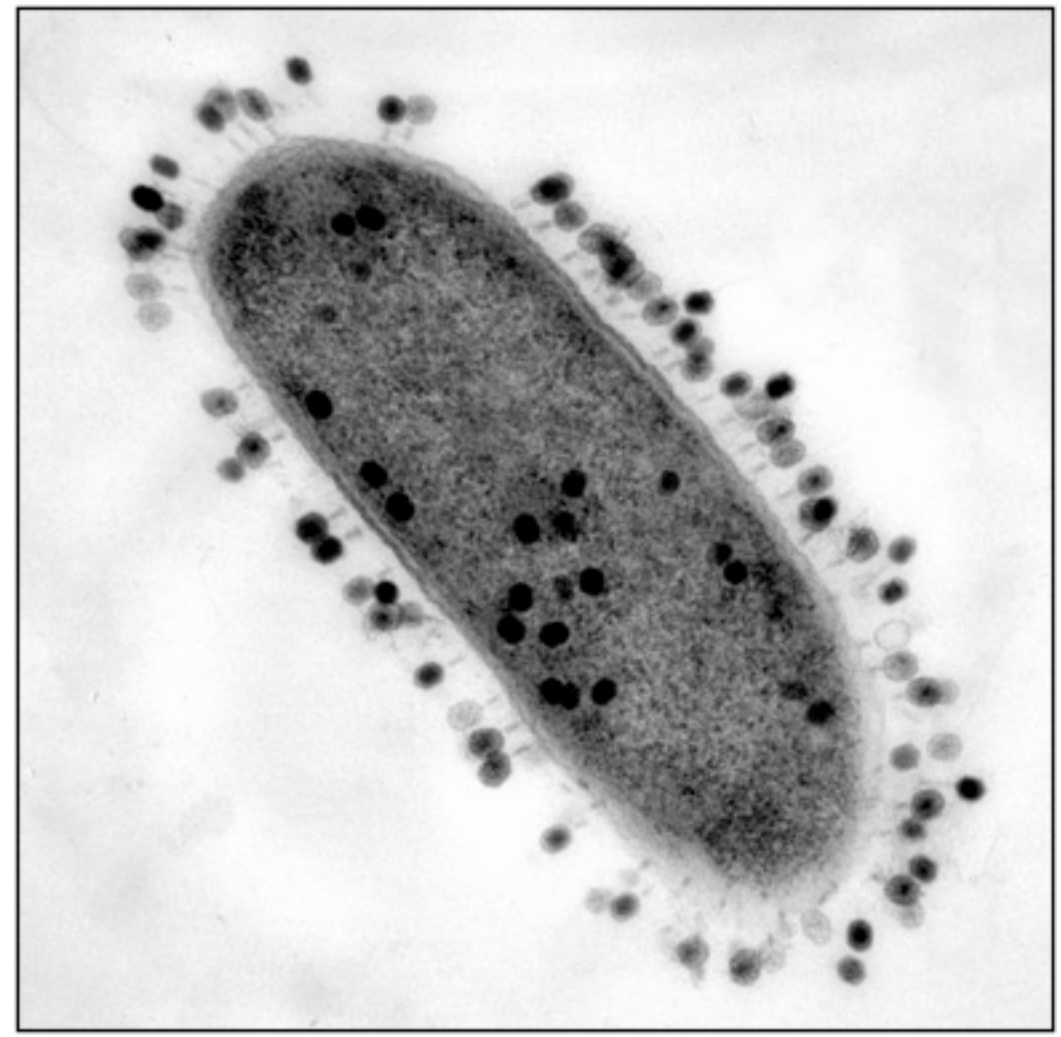
$$F_D = 20x + 8(1-x) = 8 + 12x$$

噬菌體的競爭



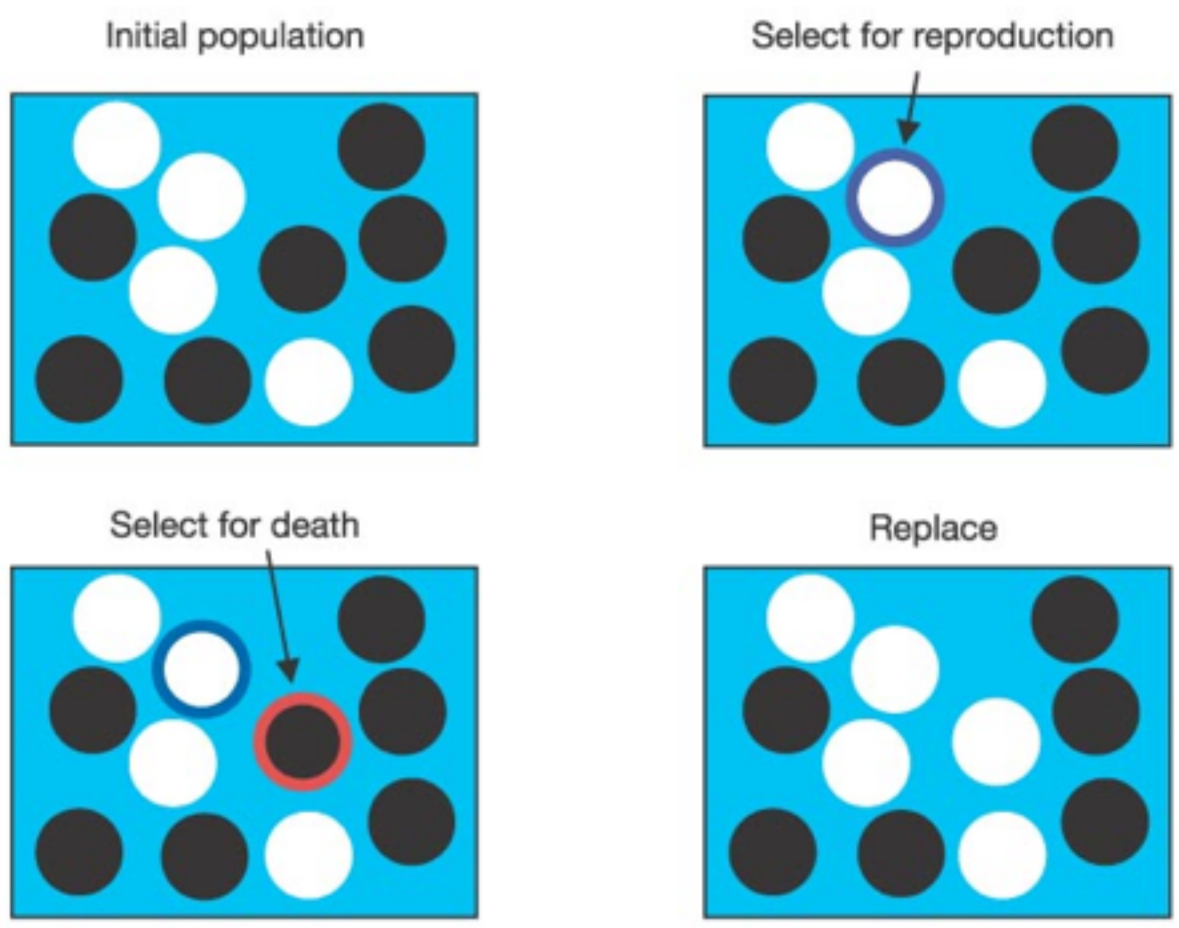
Nature **398**, 441 (1999)





自私自利的噬菌體，
有較高的競爭優勢。

Moran process



先選定一個繁衍個體，依造適應力決定繁衍機率，然後隨機取代另一個死亡個體。

replicator equations

The payoff matrix P describes the competitions between collaborators and defectors,

$$P = \begin{pmatrix} a & b \\ c & d \end{pmatrix}$$

and thus determines the replicator equations for them,

$$\boxed{\frac{dx_c}{dt} = f_c x_c - \phi x_c, \qquad \frac{dx_d}{dt} = f_d x_d - \phi x_d,}$$

where $x_c = N_c/N_{tot}$ and $x_d = N_d/N_{tot}$ are the frequencies for the collaborators and defectors. The fitness can be read off from the payoff matrix directly,

$$f_c = a x_c + b x_d, \qquad f_d = c x_c + d x_d.$$

Finally, the average fitness for the ecosystem, $\phi = f_c x_c + f_d x_d$, is a homogeneous function of order two for the variables x_c, x_d.

algorithm for MORAN

Now we turn to the algorithm for Moran process. The probability to pick C is x_c and the probability to reproduce is $0 \leq F_c \leq 1$. If we happen to pick another C for annihilation, nothing happens and N_c, N_d remain the same. However, the chance to annihilate D is x_d that leads to $(\Delta N_c, \Delta N_d) = (+1, -1)$.

Thus, the probability distribution $P(\Delta N_c, \Delta N_d)$ for the change of the populations is

$$P(+1,-1) = F_c x_c x_d, \qquad P(-1,+1) = F_d x_c x_d,$$

and $P(0,0) = 1 - P(+1,-1) - P(-1,+1)$ to ensure probability conservation. The average changes of the populations after one Monte-Carlo step are

$$\boxed{\begin{aligned} \langle \Delta N_c \rangle &= (F_c - F_d) x_c x_d, \\ \langle \Delta N_d \rangle &= (F_d - F_c) x_c x_d. \end{aligned}}$$

continuous limit

Assuming the competitions are short-ranged, there are $\mathcal{O}(N)$ reproduction-death processes in a realistic time interval. Thus, the real time and the Monte-Carlo time are related,

$$\Delta t = (\tau_0/N_{tot})\Delta\tau = \tau_0/N_{tot}.$$

In the continuous limit (or infinite-population limit), the growth rate for the collaborators is

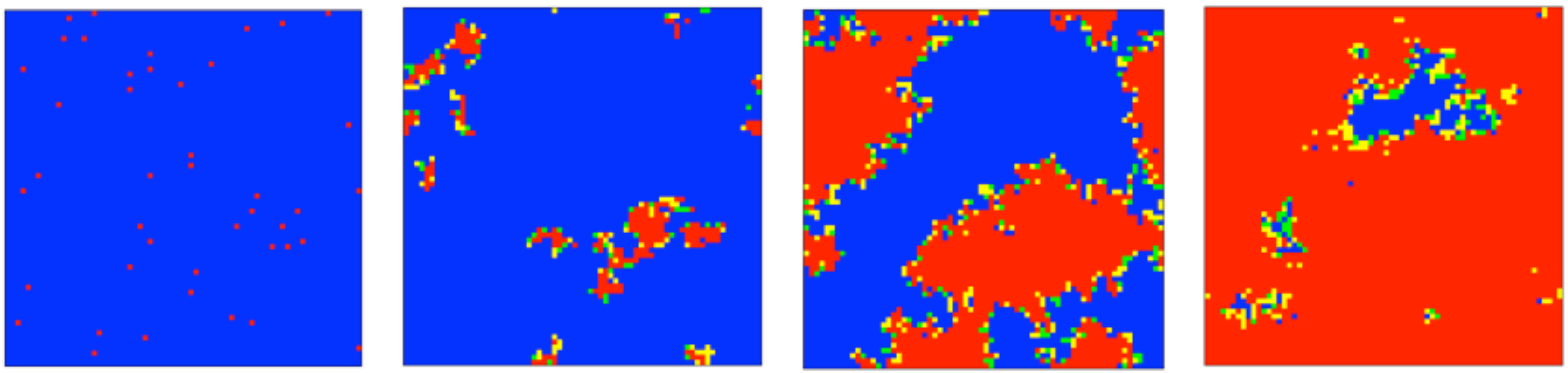
$$\frac{dx_c}{dt} \approx \frac{\Delta x_c}{\Delta t} = \frac{\langle \Delta N_c\rangle/N_{tot}}{\tau_0/N_{tot}} = \frac{\langle \Delta N_c\rangle}{\tau_0}.$$

The differential equation emergent from Moran process takes the following form,

$$\boxed{\frac{dx_c}{dt} = x_c x_d(f_c - f_d),}$$

where the fitness is $f_i = F_i/\tau_0$. This may look different from the replicator equation. But, after some algebra, it is straightforward to show that they are identical (up to stochastic fluctuations).

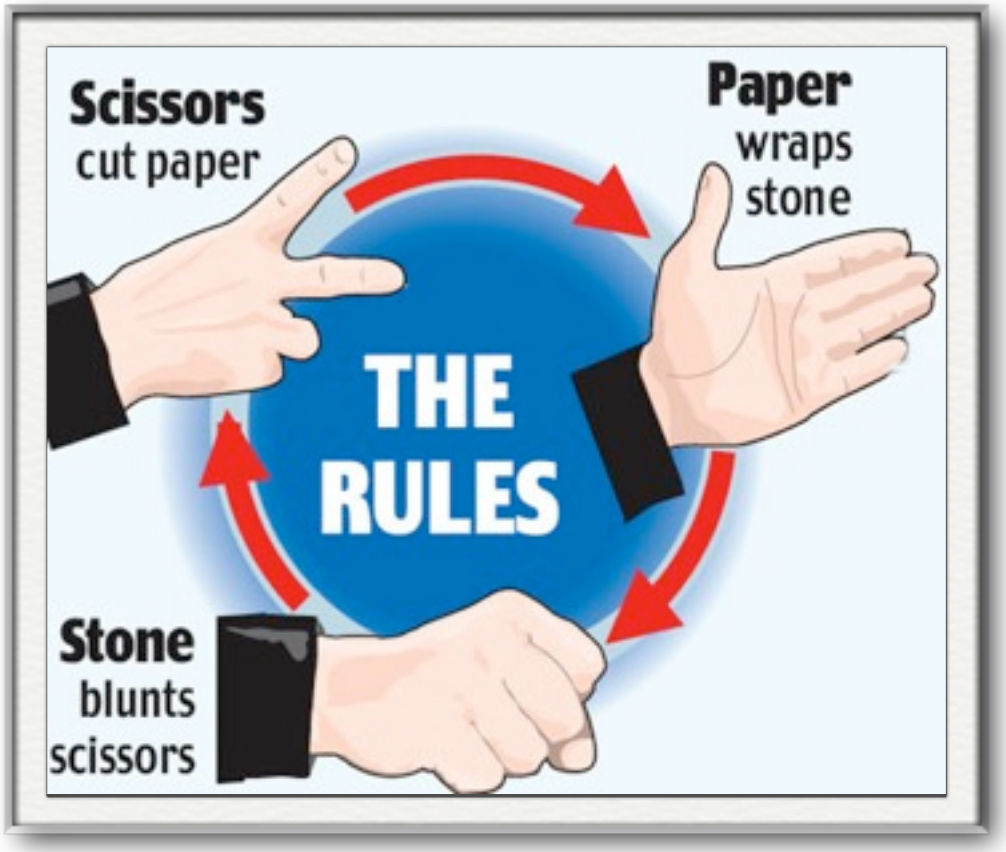
幾顆老鼠屎⋯



一開始自私者分布零散，接著慢慢形成小集團，再漸漸連結成大集團。最後，一統江湖！

自然界的剪刀石頭布

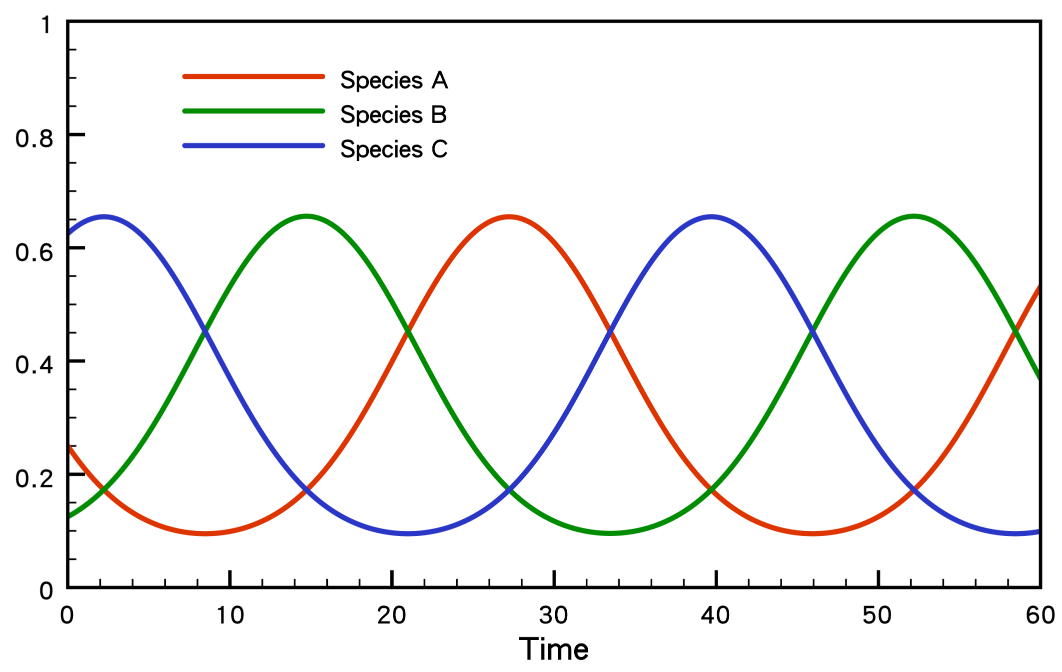
剪刀石頭布

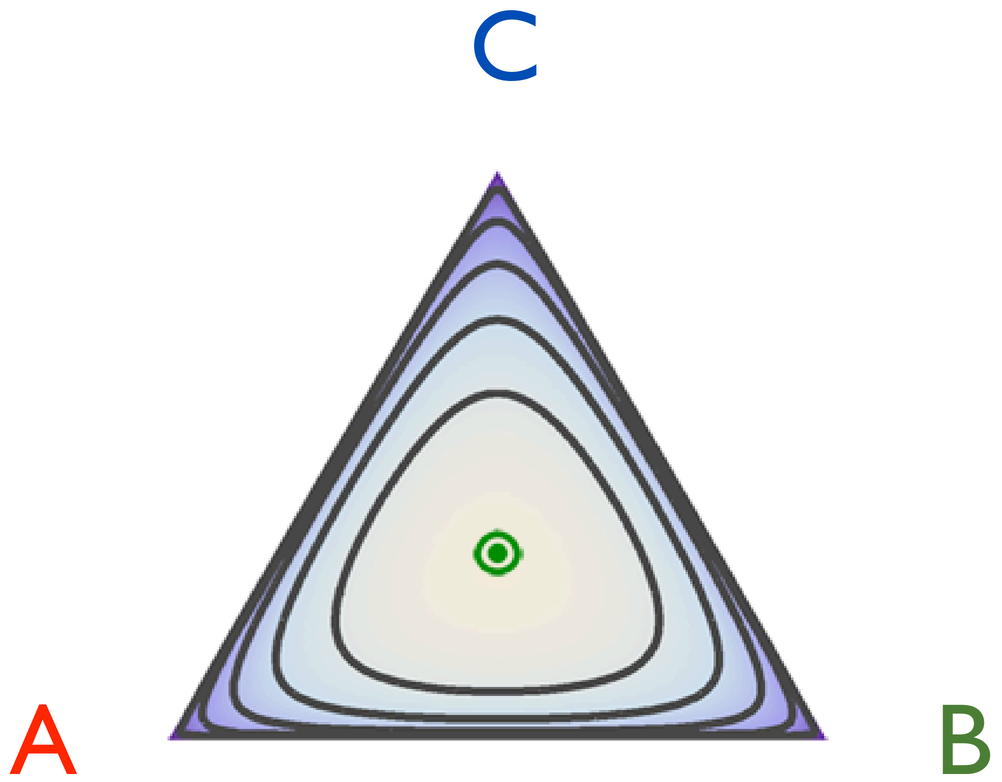


將有助於生物多樣性？
還是增加生態系的不穩
定性，而導致滅絕？

複雜的掠食關係

演化軌跡





三個環狀相剋的物種，族群數量會隨著時間震盪，而達成微妙的生態平衡。

蜥蜴玩剪刀石頭布？

Nature **380**, 240 (1996)

印第安那的學者跑到加州抓蜥蜴，發現他們在陽光下大玩剪刀石頭布。

各色公蜥蜴

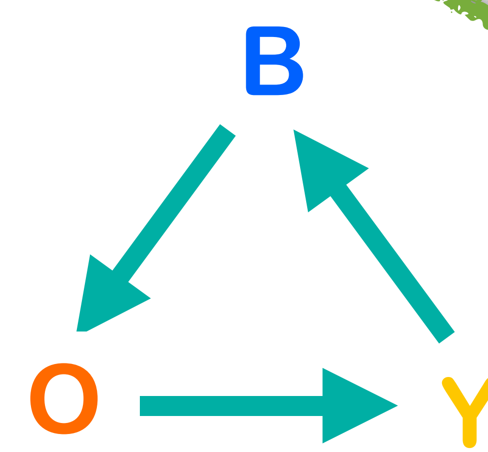
Nature **380**, 240 (1996)

橘色、藍色、黃色公蜥蜴以不同戰略，來取得最佳化的交配機會。

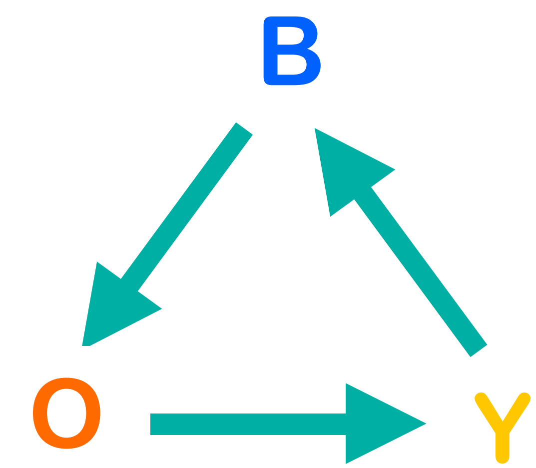
O：霸王蜥

B：愛家蜥

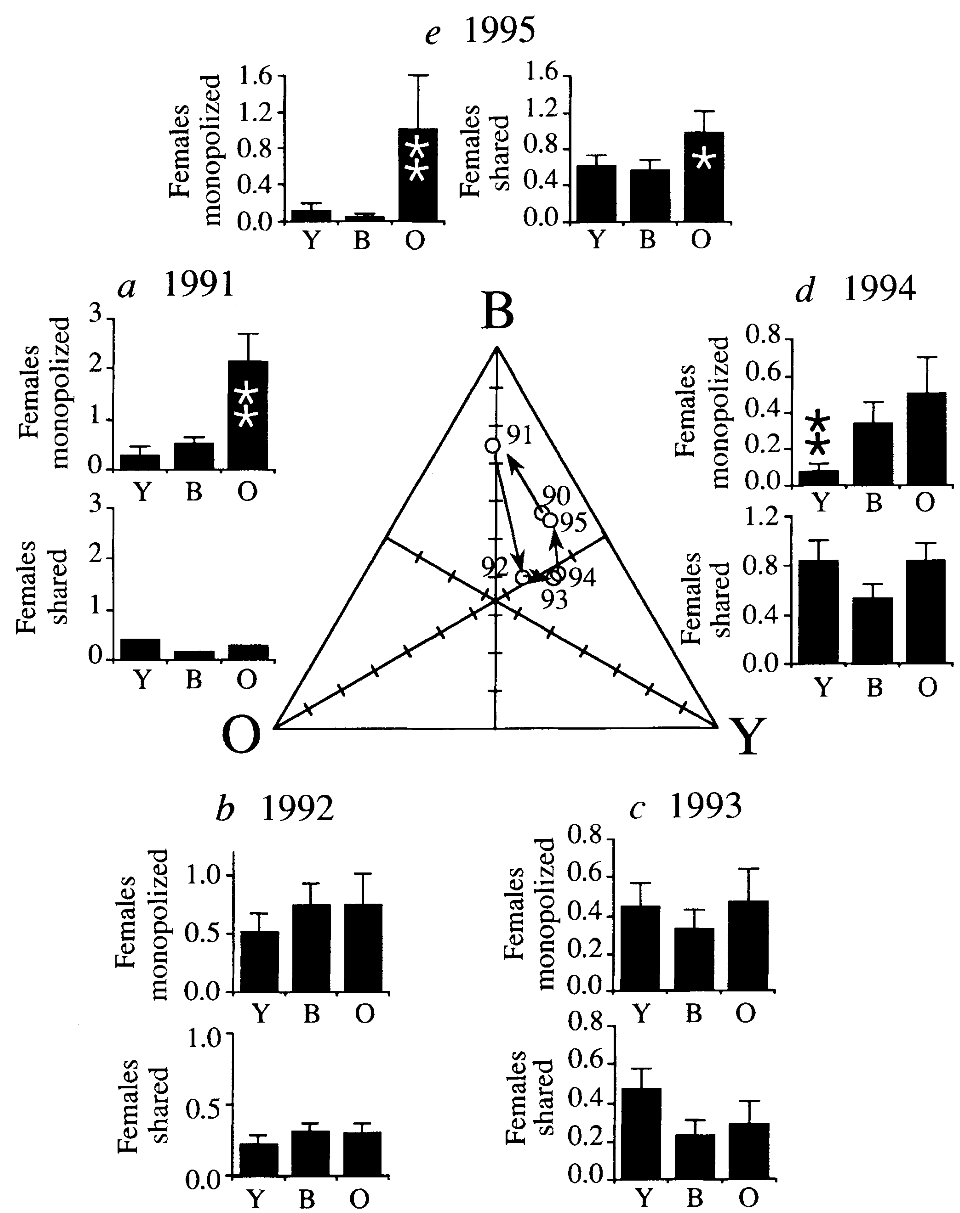
Y：偷情蜥

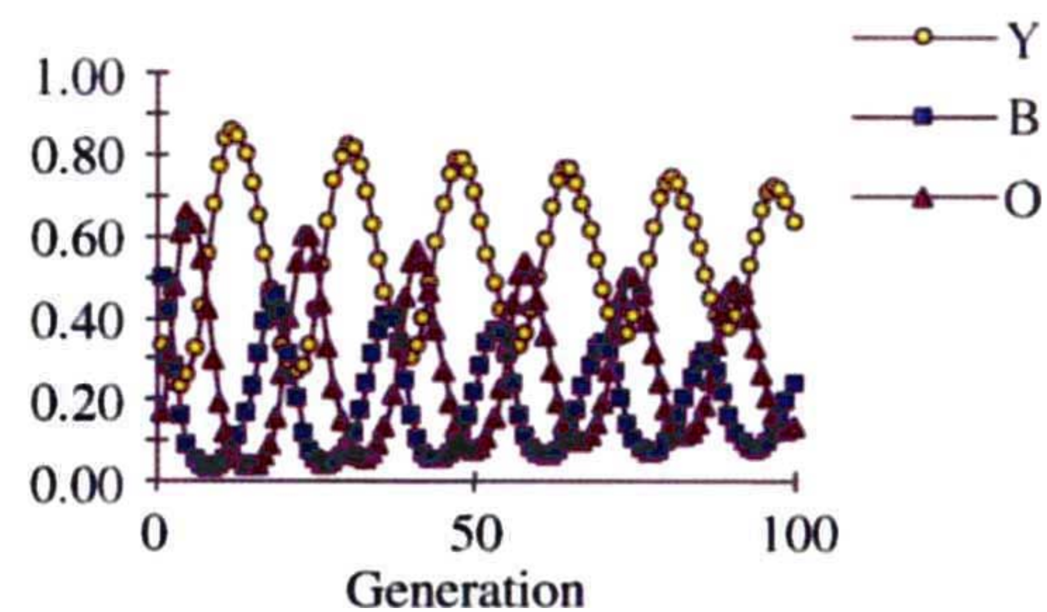


消長互見



Nature **380**, 240 (1996)





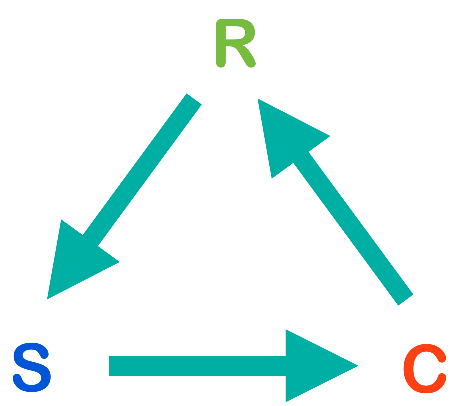
在不同戰略下，各色公蜥蜴數量消長互見，呈現震盪的現象。

結果，細菌也愛玩

Nature **418**, 171 (2002)

加州的學者在實驗室中發現，大腸桿菌也在玩剪刀石頭布的遊戲。

細菌的世界

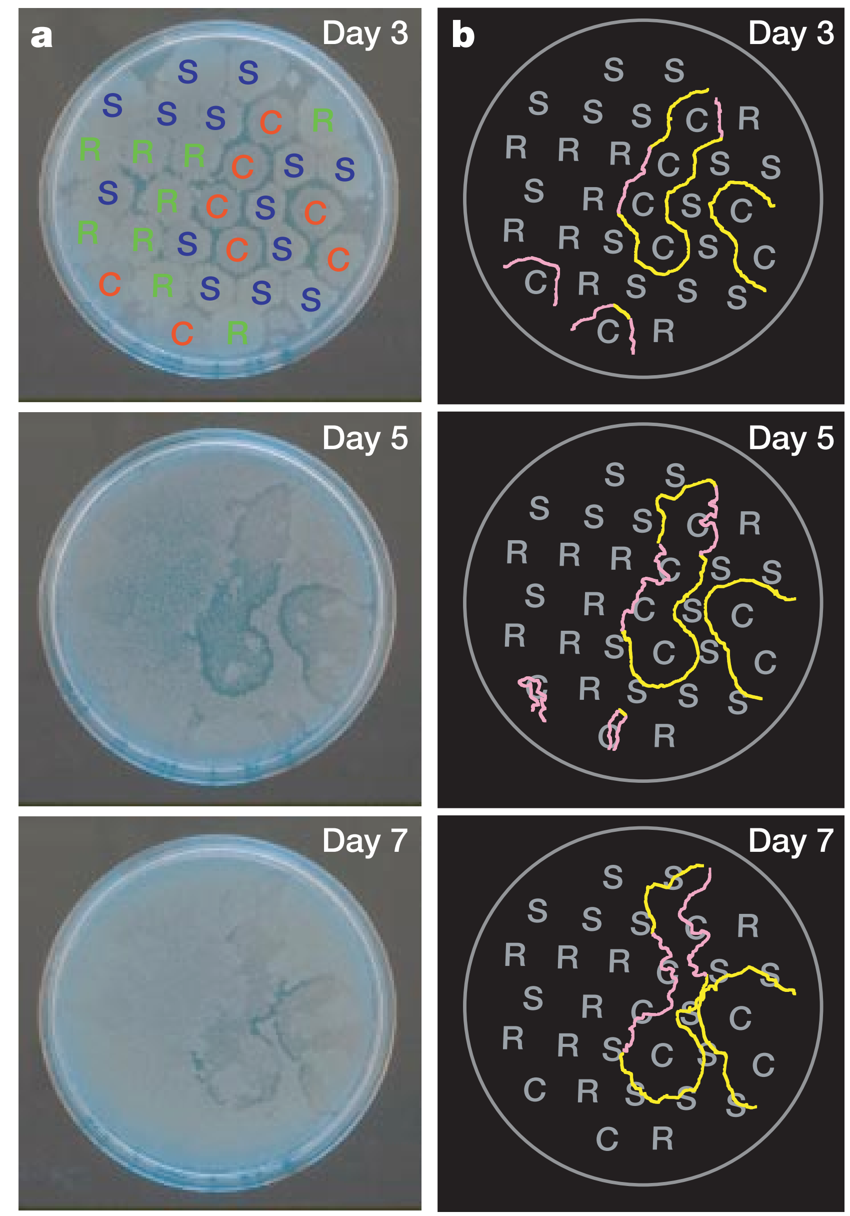


C : 激進恐怖菌

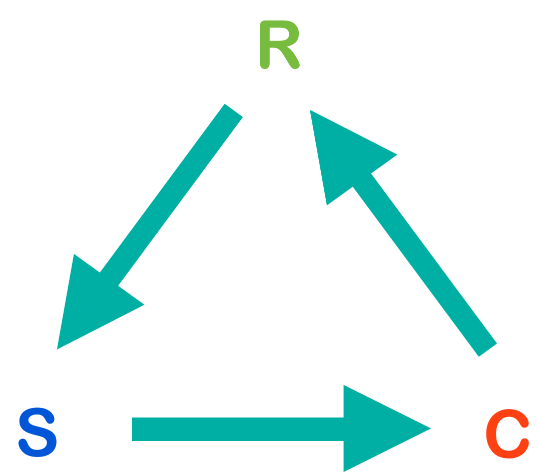
R : 憂天杞國菌

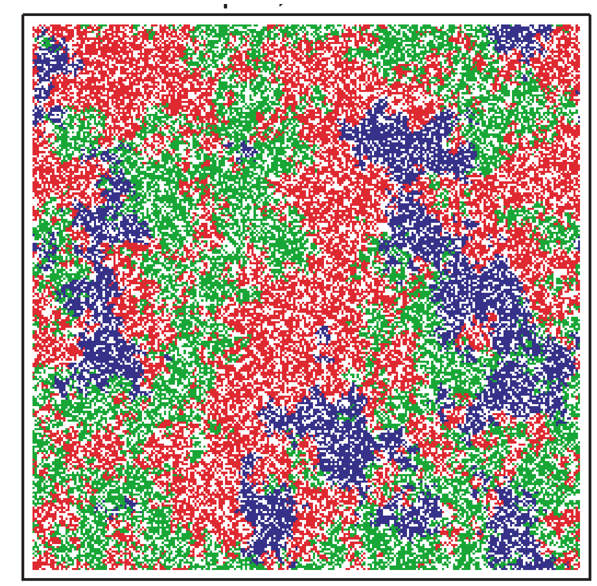
S : 平菌老百姓

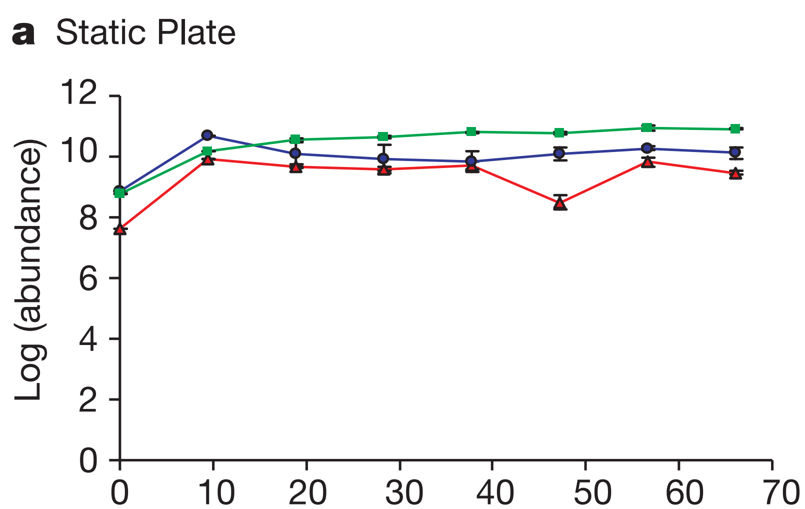
Nature **418**, 171 (2002)



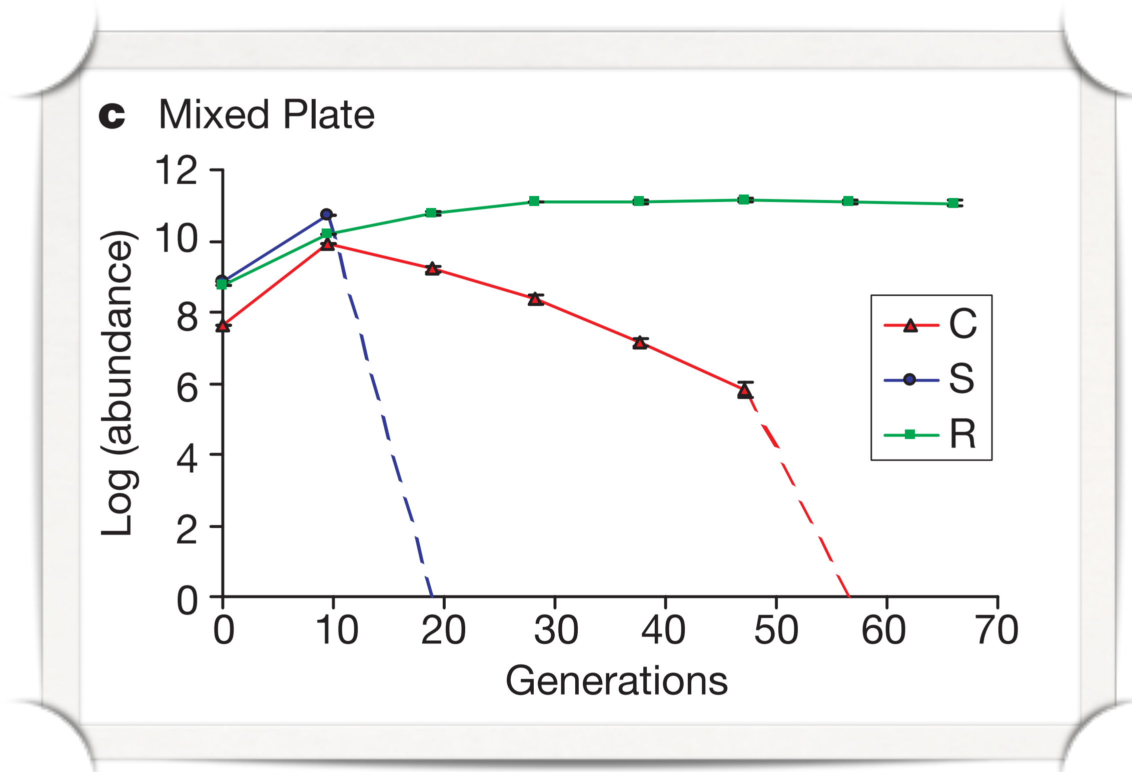
絕種了…



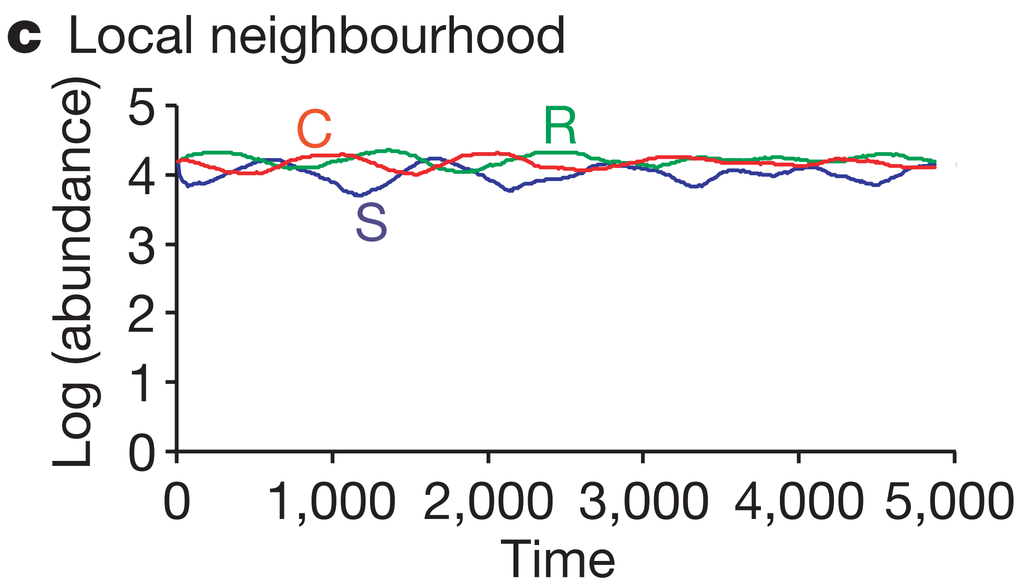


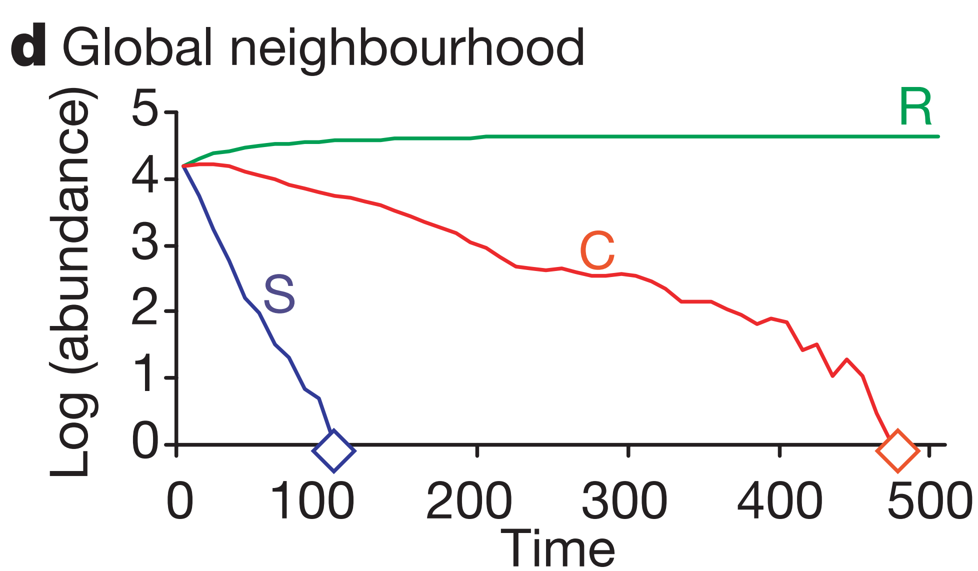


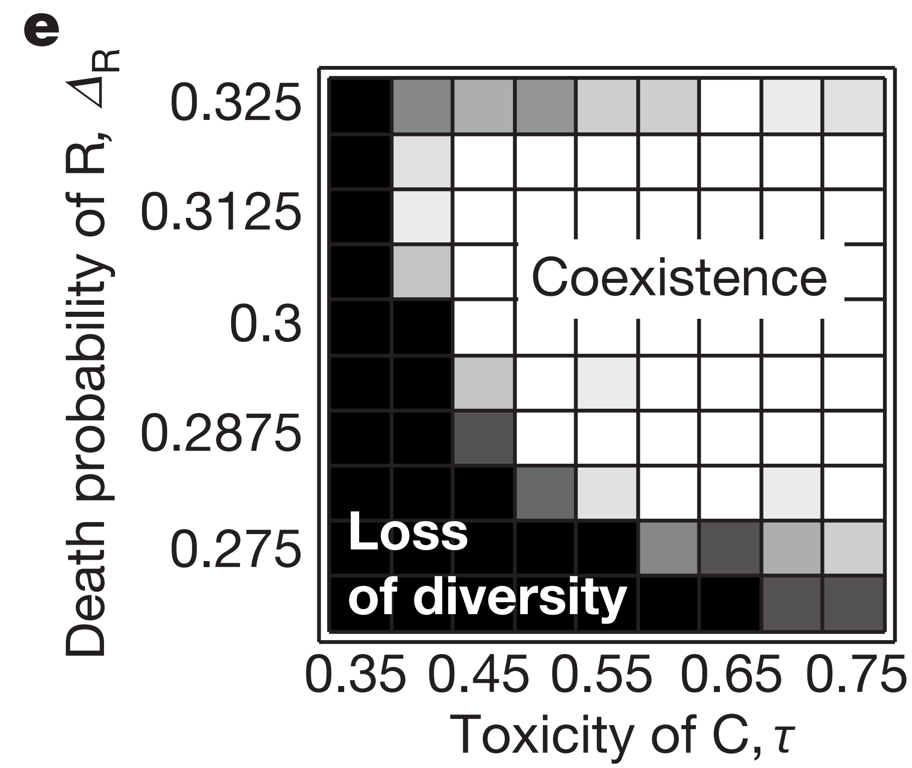
混在一起的細菌們，彼此競爭的結果，最後僅有一種生存下來，其它兩種都滅絕了…



不同的下場







數值模擬的結果，的確得到類似的現象。族群數量是整數，為什麼會如此重要？

細菌快跑

Nature **448**, 1046 (2007)

物種遷移反而摧毀生態平衡

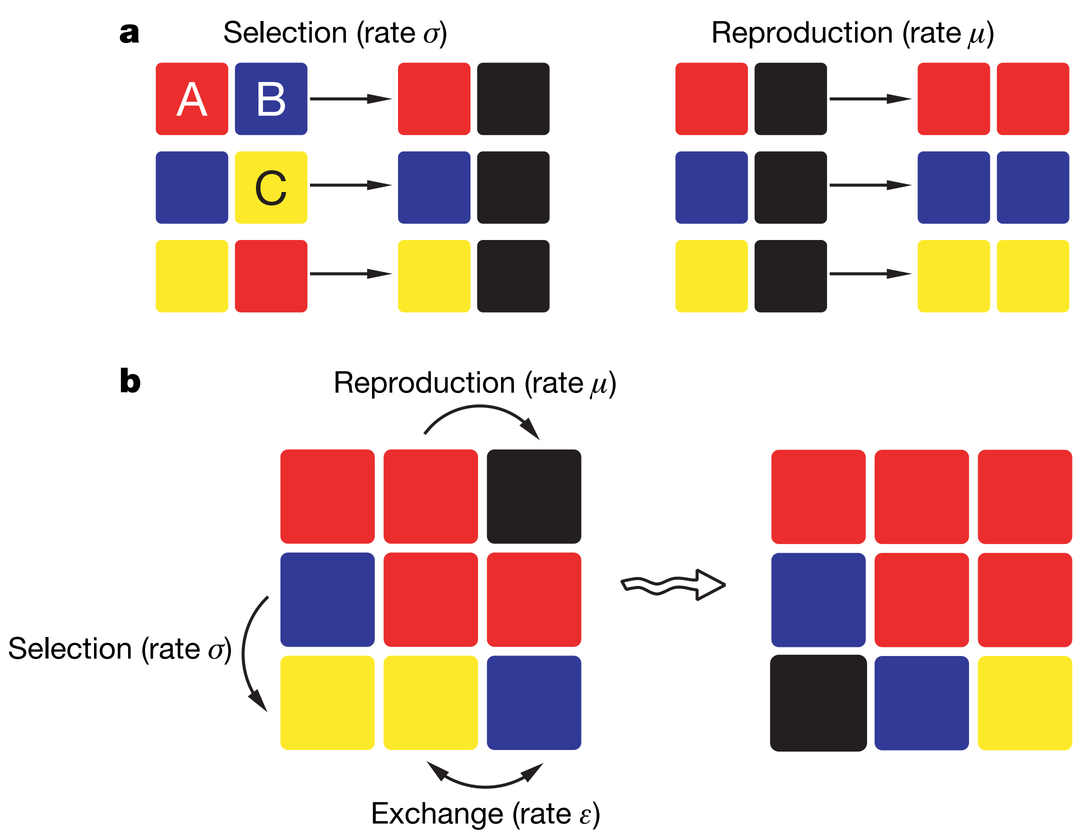
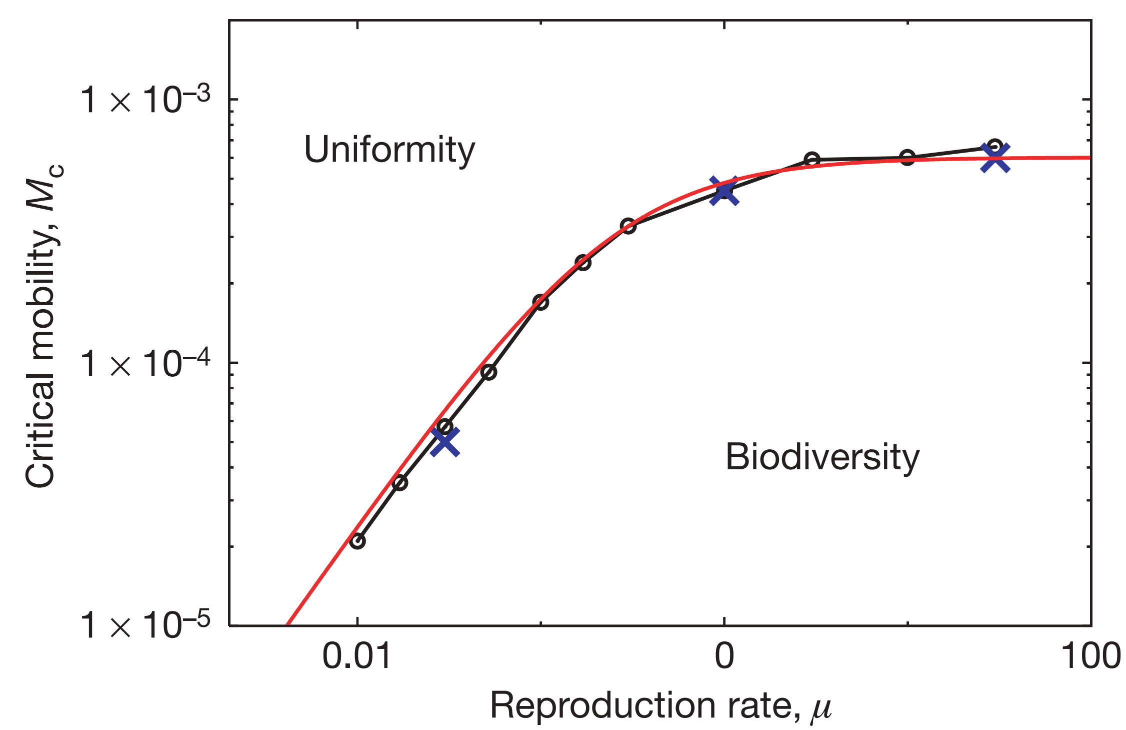
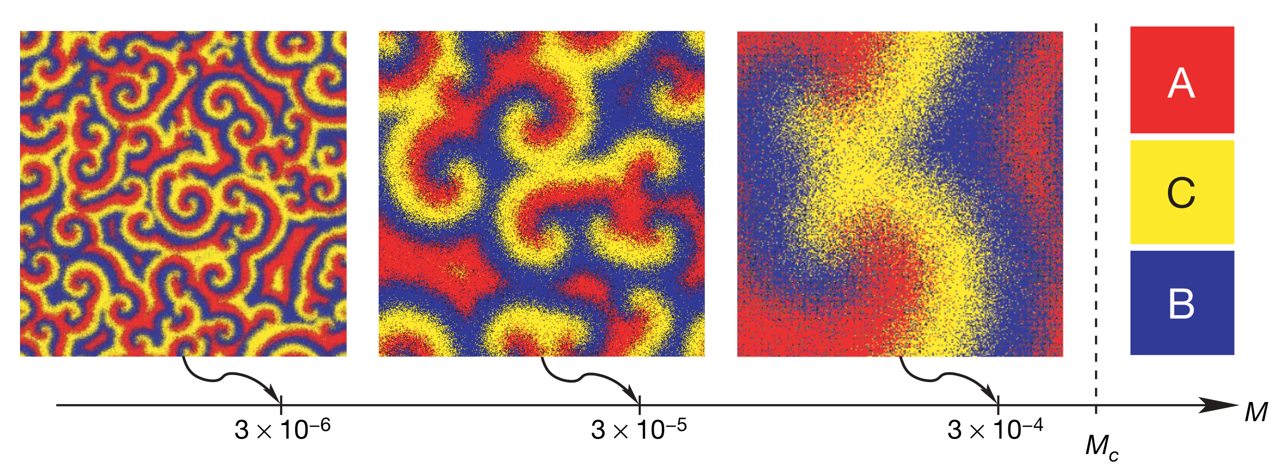


Figure 1 | The rules of the stochastic model. Individuals of three competing species A (red), B (blue), and C (yellow) occupy the sites of a lattice. **a**, They interact with their nearest neighbours through selection or reproduction, both of which reactions occur as Poisson processes at rates σ and μ, respectively. Selection reflects cyclic dominance: A can kill B, yielding an empty site (black). In the same way, B invades C, and C in turn outcompetes A. Reproduction of individuals is only allowed on empty neighbouring sites, to mimic a finite carrying capacity of the system. We also endow individuals with mobility: at exchange rate ε, they are able to swap position with a neighbouring individual or hop onto an empty neighbouring site (exchange). **b**, An example of the three processes, taking place on a 3×3 square lattice.





多樣性 v.s. 滅絕

There's still a long way to understand biodiversity and extinction!