生態系制御に関する数理モデル解析

～ 人間の介入の効果を含む個体群動態の基礎理論 ～

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Outline

Prologue

Implication from Mathematical Models

- Mathematical Model for Harvesting/Thinning
- Species Deletion/Introduction

Concluding Remarks

Prologue

Pest control

Application of a pesticide for a pest control

Pest control

Application of a pesticide for a pest control

$$\Downarrow$$

Pest outbreak in a later period
after the pesticide introduction

Pest control

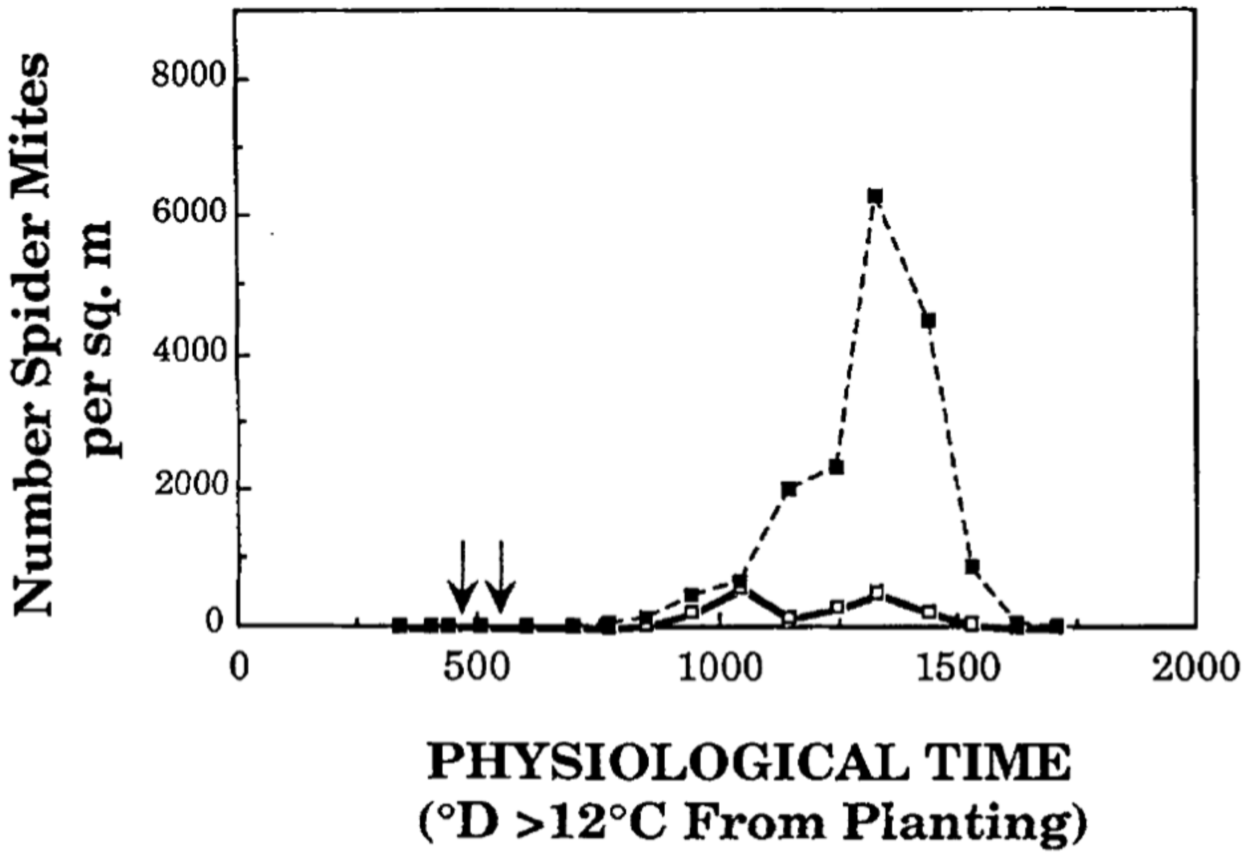


Fig. 2. Effect of two permethrin applications on spider mite density (adults + immatures) during a field experiment conducted in the San Joaquin Valley of California in 1982: - -■- - permethrin; —□— untreated; arrows represent times of permethrin applications.

FROM: Trichilo, P. J. and L. T. Wilson, 1993. An ecosystem analysis of spider mite outbreaks: physiological stimulation or natural enemy suppression. *Exp. Appl. Acarol.* **17**: 291–314.

└ Pest control

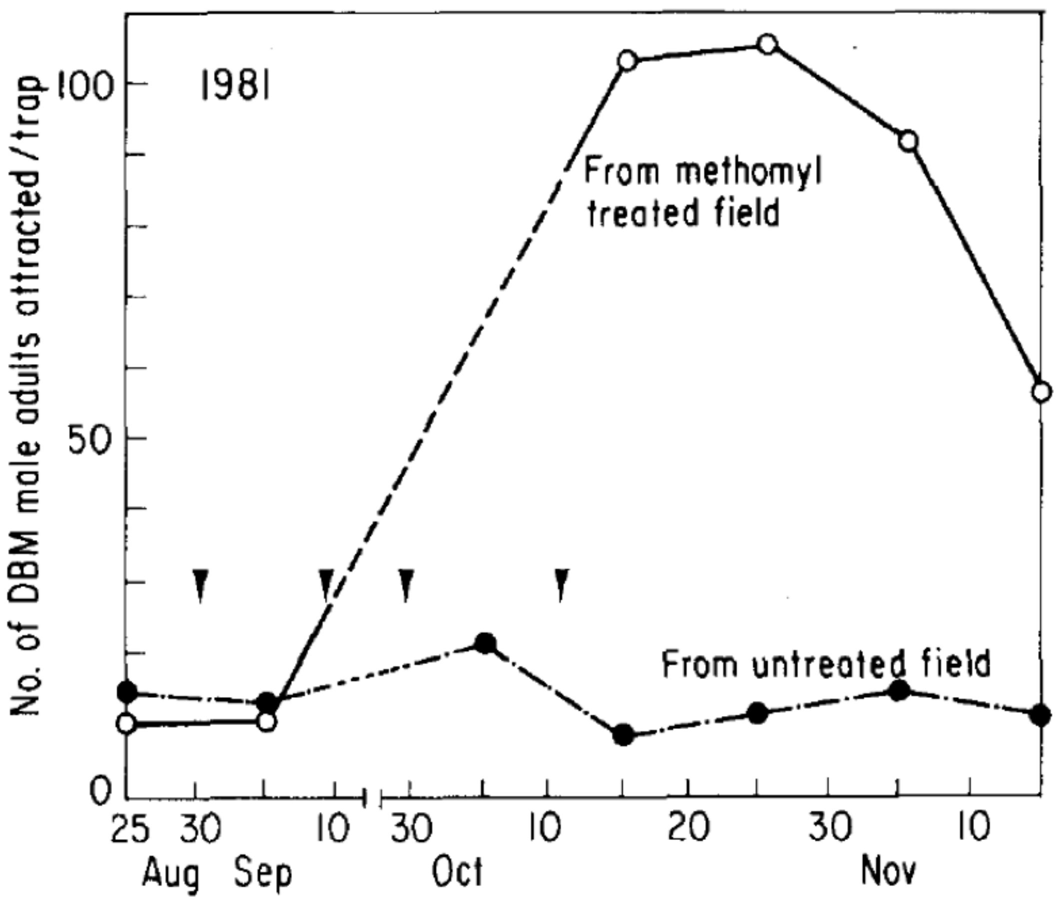


Figure 1.
Effects of methomyl treatments on the diamondback moth populations captured in pheromone traps from cauliflower fields of SHES. Three dry type traps (made by Takeda Chemical Ind Ltd) baited with "Px" (a synthetic sex pheromone for *P. xylostella*, which is a mixture of 0.05 mg of (Z)-11 hexadecenal with 0.05 mg of (Z)-11 hexadecenyl acetate and 0.001 mg of (Z)-11 hexadecenol) were arranged in each field. ▼: date of treatment

FROM: Nemoto, H. 1986. Factors inducing resurgence in the diamondback moth after application of methomyl. In: N.S. Talekar and T.D. Griggs (eds), *Diamondback moth management: Proceedings of First International Workshop*. Asian Vegetable Research and Development Center, Tainan, Taiwan. pp. 387–394.

└Pest control

Causes of the pest resurgence:

- Emergence of the pesticide-resistant strain;
- Decrease of the enemy population;
- Shift of the pesticide-applied crop condition (trophobiosis);
- Physiological increase of the pest fecundity (hormesis, homoligosis).

However, we can theoretically suggest:

The paradox of pest control may be caused only by the native ecological reaction disturbed by the pest control.

└ **In more general context**

Application of an operation to reduce the population size of target species

$$\Downarrow$$

Eventual increase of the target population size after undergoing the operation

cf. hydra effect

Biological operations

- Species deletion/isolation;
- Species introduction (e.g. genetically operated);
- Biotope/ecotope;
- Ecological service

Focus of this talk

Operation for population size

Focus of this talk

Operation for population size may cause some unexpected/paradoxical consequence.

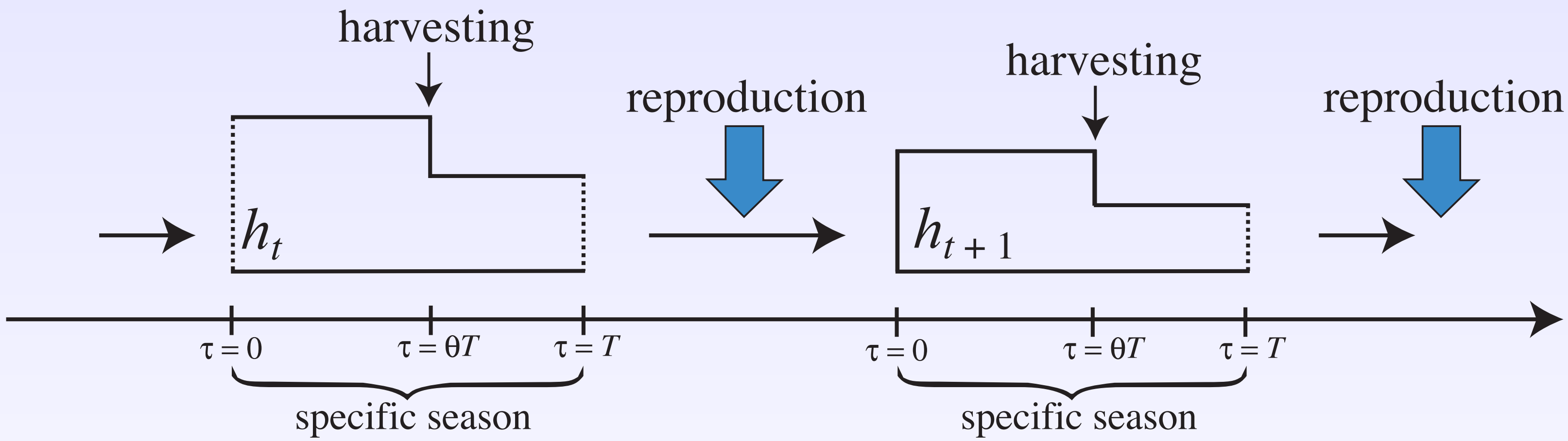
Focus of this talk

Operation for population size may cause some unexpected/paradoxical consequence.

To control a population size, we may utilize such paradoxical feature of the ecological system which the target population belongs to.

Mathematical Models and Results

Modeling



Scheme of the population dynamics with harvesting/thinning. h_t is the population density at the beginning of the t th specific season in which the harvesting/thinning is applied.

Mathematical Model for Harvesting/Thinning

Mathematical model

$$h_{t+1} = \lambda \left\{ \theta R(h_t) + (1-\theta) R((1-\rho)h_t) \right\} (1-\rho) h_t$$

└Mathematical Model for Harvesting/Thinning

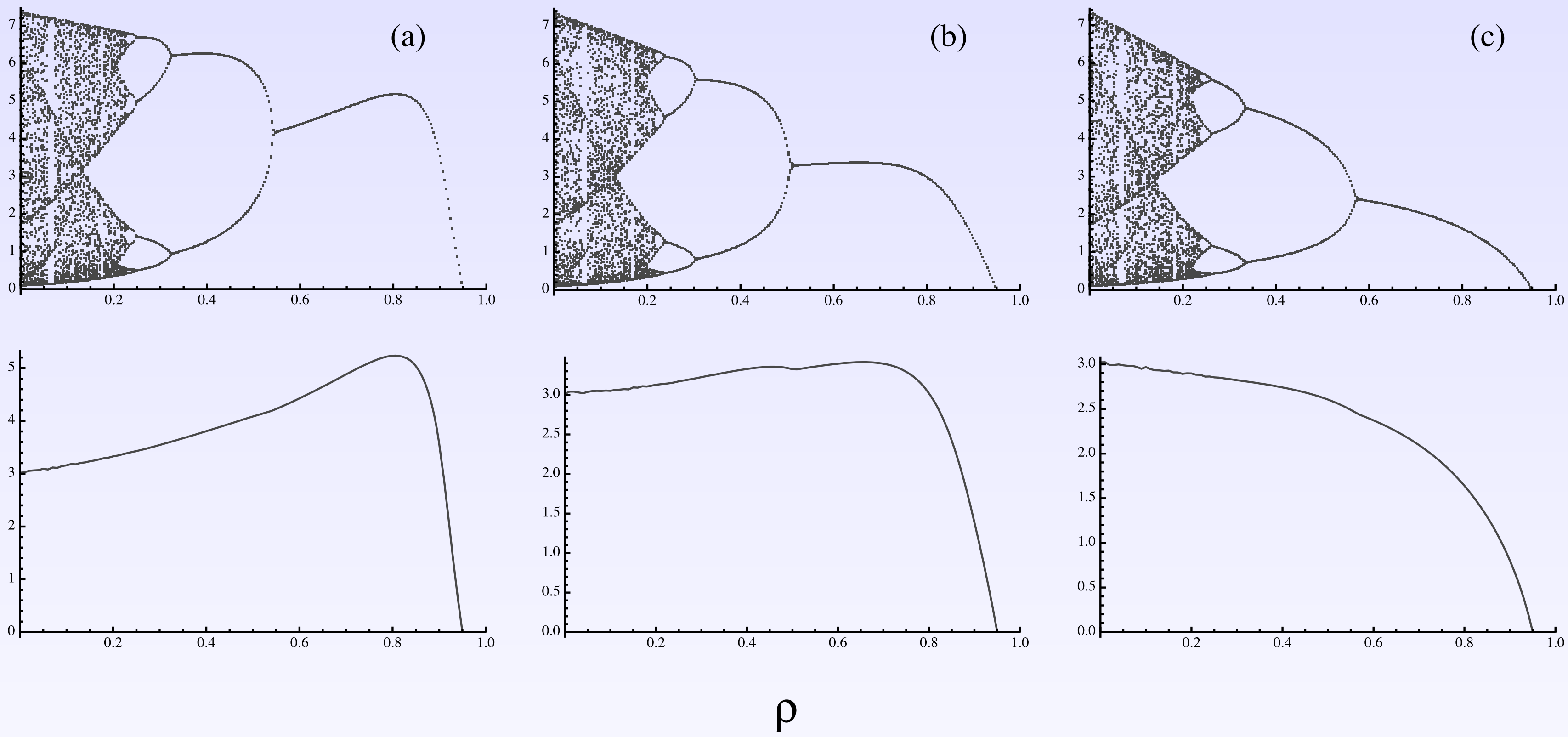
Mathematical model

$$h_{t+1} = \lambda \left\{ \theta R(h_t) + (1-\theta) R((1-\rho)h_t) \right\} (1-\rho) h_t$$

Ricker type of reproduction function

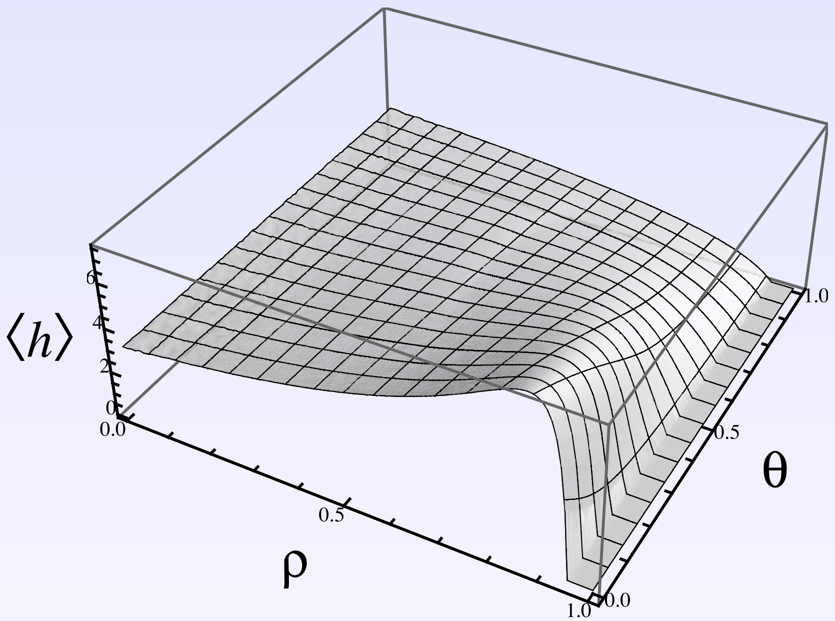
$$R(h) = \mathrm{e}^{-\beta h}$$

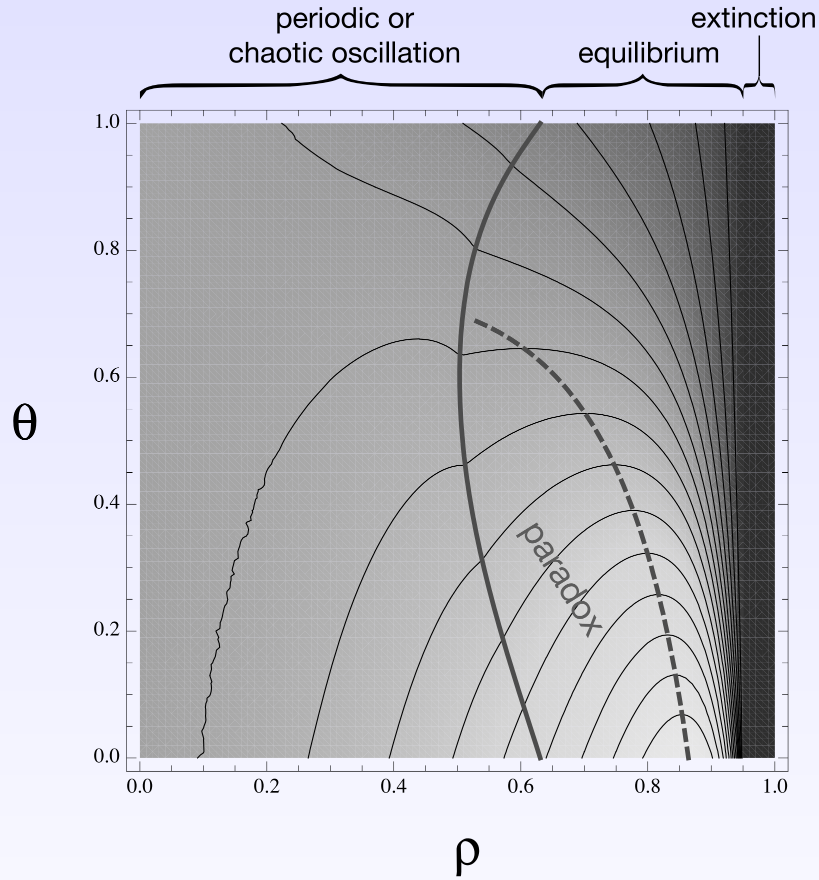
└Mathematical Model for Harvesting/Thinning



Bifurcation diagrams and the time-averaged values in terms of ρ. Numerically drawn for the Ricker type of reproduction function $R(h) = \mathrm{e}^{-\beta h}$. (a) $\theta = 0.3$; (b) $\theta = 0.6$; (c) $\theta = 0.9$. Commonly $\beta = 1.0$ and $\lambda = 20.0$. In each case, the upper is the bifurcation diagram and the lower the time-averaged value.

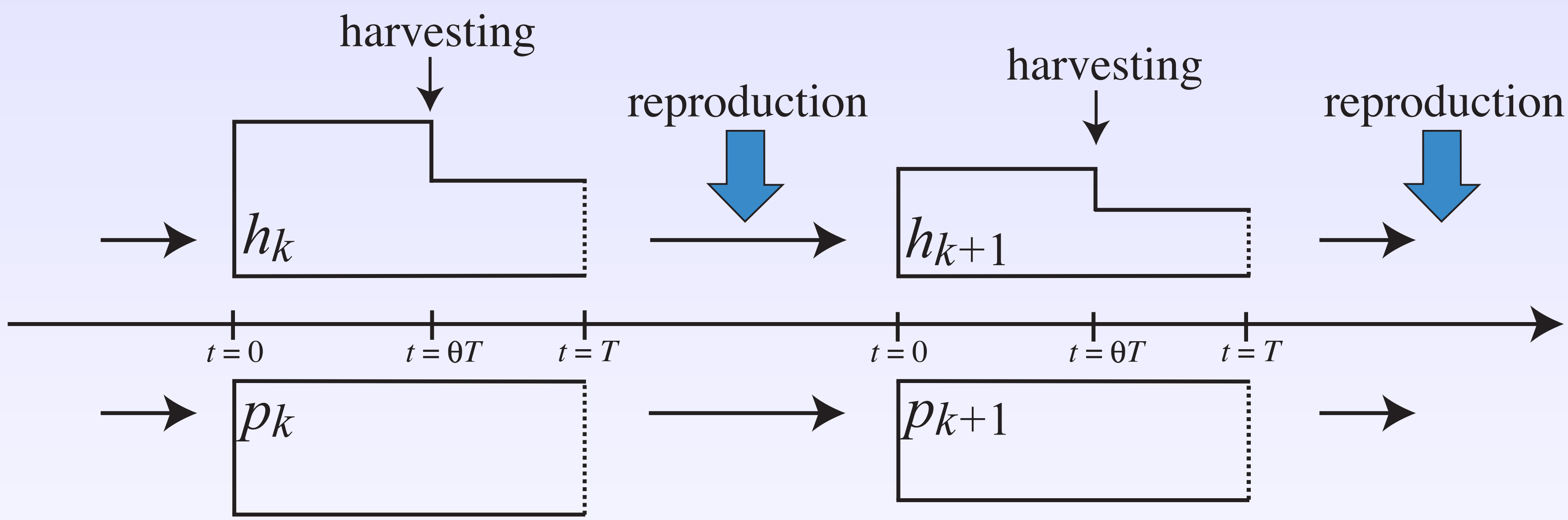
└Mathematical Model for Harvesting/Thinning





(ρ,θ)-dependence of the time-averaged population size $\langle h\rangle$ in the sufficiently later generations. Numerically drawn for the Ricker type of reproduction function $R(h) = \mathrm{e}^{-\beta h}$ with $\beta = 1.0$ and $\lambda = 20.0$. In the density plot, the lighter region indicates the larger time-averaged population size $\langle h\rangle$.

Modeling with natural enemy



Scheme of the population dynamics under harvesting/thinning effect in our model. h_k is the target population density and p_k is the (natural) enemy population density at the beginning of the k th predation/parasitism season. The harvesting/thinning has no direct effect on the enemy population.

└Mathematical Model for Harvesting/Thinning

Mathematical model

$$
\begin{aligned}
h_{k+1} &= \lambda S_{\theta,\rho}(h_k)(1-\rho)\Pi(p_k)h_k; \\
p_{k+1} &= \mu(1-\rho)\{1-\Pi(p_k)\}h_k;
\end{aligned}
$$

$$
S_{\theta,\rho}(h_k) = \theta R(h_k) + (1-\theta)R((1-\rho)h_k).
$$

cf. Nicholson–Bailey model

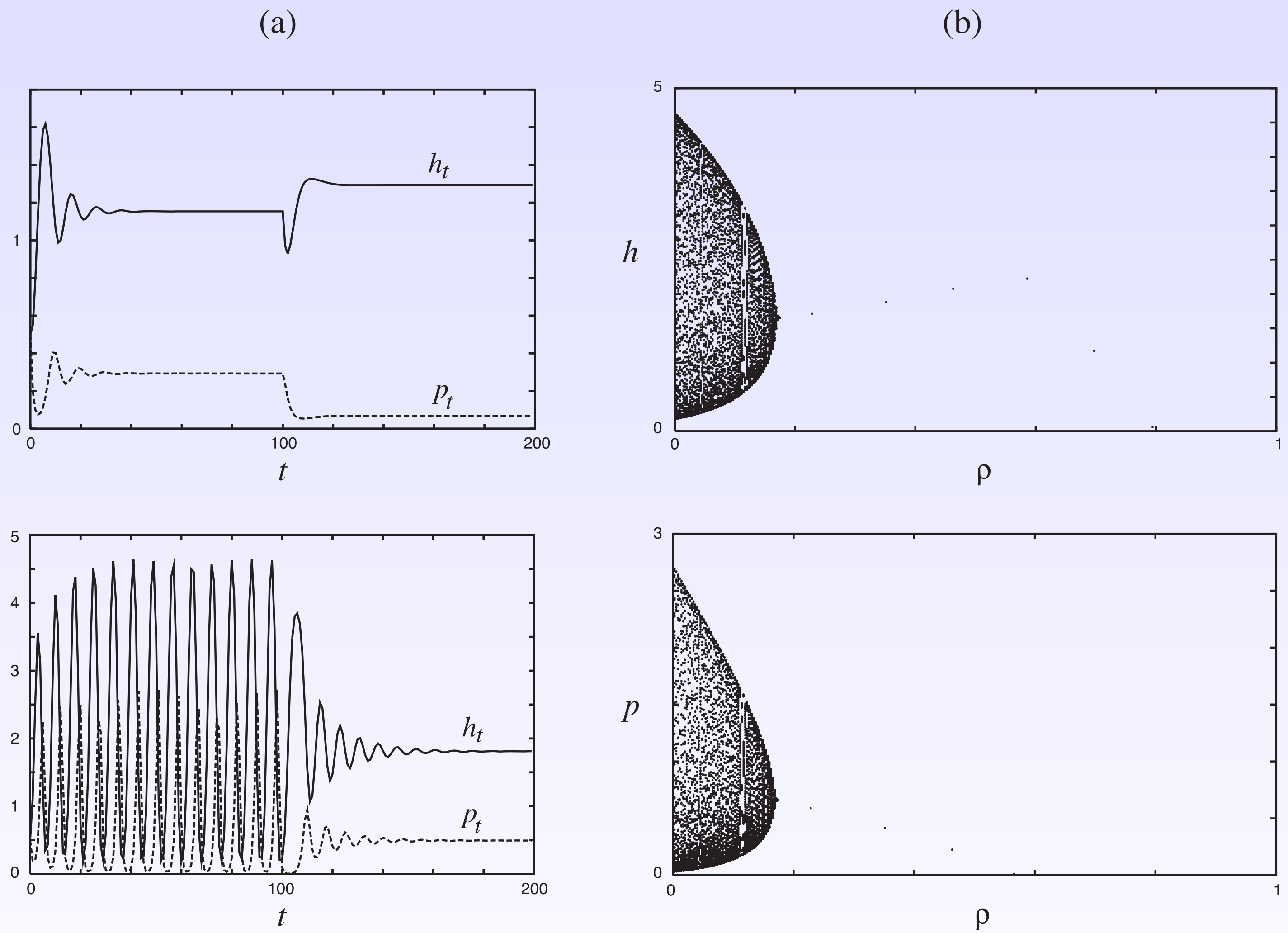
└Mathematical Model for Harvesting/Thinning

Assumptions for the mathematical model:

- $R(0) = 1$ and $\lim_{h \to \infty} R(h) = 0$;
- $R'(h) < 0$ for any $h > 0$;
- $\Pi(0) = 1$ and $\lim_{p \to \infty} \Pi(p) = 0$;
- $\Pi'(p) < 0$ and $\Pi''(p) \geq 0$ for any $p \geq 0$,

where $R'(h) = dR(h)/dh$, $\Pi'(p) = d\Pi(p)/dp$, and $\Pi''(p) = d^2\Pi(p)/dp^2$.

└Mathematical Model for Harvesting/Thinning



Numerical illustrations of the paradox emergence for the model with an exponential function $\Pi(p) = e^{-\alpha p}$ and Beverton–Holt type function $R(h) = 1/(1 + bh)$. (a) population size transition by the introduction of harvesting for the host. $\alpha = 1$; $\mu = 1$; $b = 0.75$; $\theta = 0.5$. Upper: $\lambda = 2.5$ and $\rho = 0.2$, lower: $\lambda = 5.0$ and $\rho = 0.3$. The harvesting starts after $t = 100$. In the lower case, the chaotic oscillation transits to a dumping oscillation toward an equilibrium. (b) Numerically obtained bifurcation diagram: ρ-dependence of the limit state as $t \to \infty$. $\alpha = 1$; $\mu = 1$; $\lambda = 5.0$; $b = 0.75$; $\theta = 0.5$.

Mathematical Model for Harvesting/Thinning

Mathematical result:

The paradox of pest control can occur if and only if

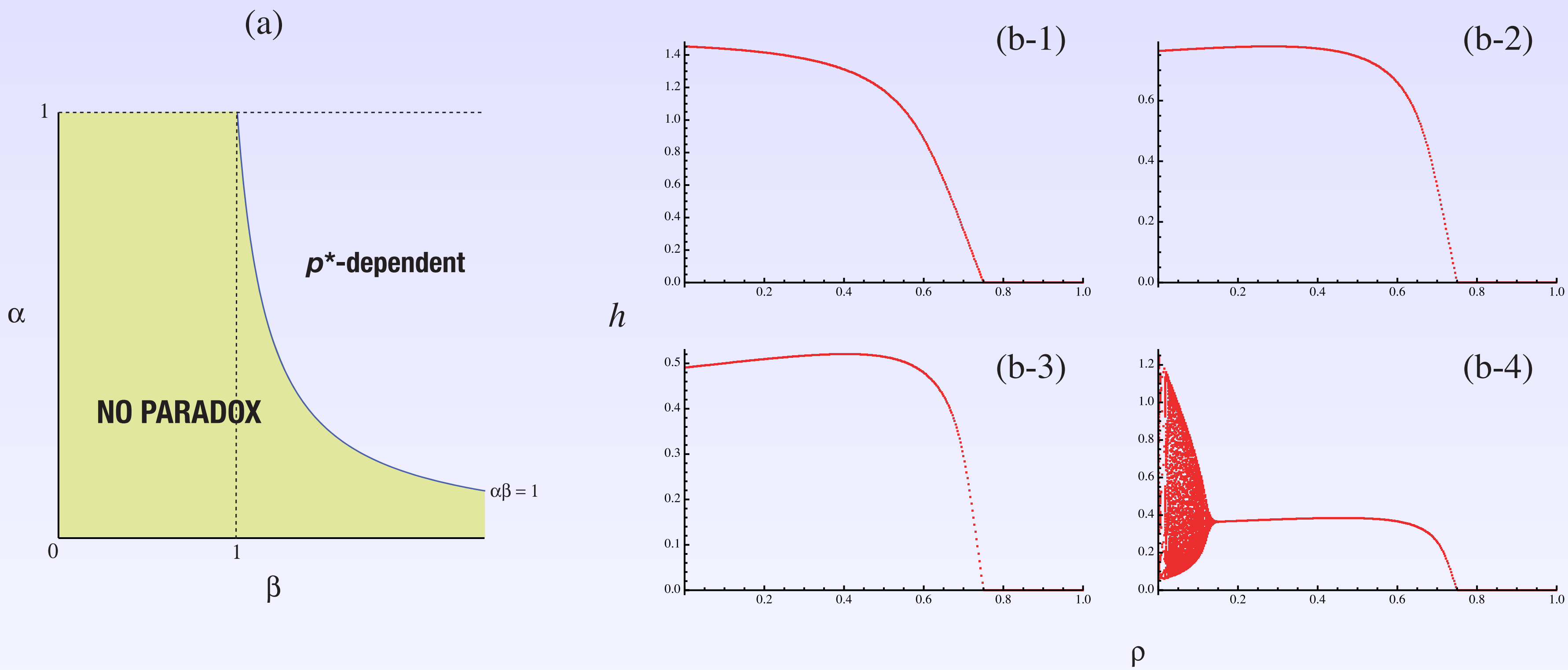
$$\theta R\left(\frac{Q(p^*)}{1-\rho}\right) \frac{d}{dp}\{Q(p)\Pi(p)\}\Big|_{p=p^*} + (1-\theta)\frac{d}{dp}\{R(Q(p))Q(p)\Pi(p)\}|_{p=p^*} < 0$$

for some $\rho > 0$, where $Q(p) := p/[\mu\{1-\Pi(p)\}]$ that is monotonically increasing in terms of p.

└Mathematical Model for Harvesting/Thinning

The paradox is *more likely to occur* with the harvesting *before or earlier* in the predation/parasitism season.

└Mathematical Model for Harvesting/Thinning



(a) **Analytical result about the paradox emergence with the general concave rational function $\Pi(p) = 1/(1+Cp^{\alpha})^{\beta}$, in case of $\theta = 1$.** For (α, β) of the region indicated by "NO PARADOX", the paradox never occurs. For (α, β) of the white region indicated by "p^*-dependence", the paradox emergence depends on the features of the density effect function R and on the other parameter values. The nontrivial equilibrium (h^*, p^*) always exists. (b) **Numerically drawn ρ-dependence of the limiting state of h_k ($k \gg 1$) with the general concave rational function and the Beverton–Holt type density effect function $R(h) = 1/(1+bh)$.** $\theta = 0.5$; $\lambda = 4.0$; $\mu = 1.0$; $b = 1.0$; $C = 1.0$; $\alpha = 0.8$. (b-1) $\beta = 1.0$; (b-2) $\beta = 2.0$; (b-3) $\beta = 3.0$; (b-4) $\beta = 4.0$.

└Mathematical Model for Harvesting/Thinning

Not a few cases of the paradox of pest control may be caused only by the native ecological reaction disturbed by the pest harvesting, even with no harvesting-resistance, no hormesis, and no direct effect on its natural enemy and food.

└ Mathematical Model for Harvesting/Thinning

Not a few cases of the paradox of pest control may be caused only by the native ecological reaction disturbed by the pest harvesting, even with no harvesting-resistance, no hormesis, and no direct effect on its natural enemy and food.

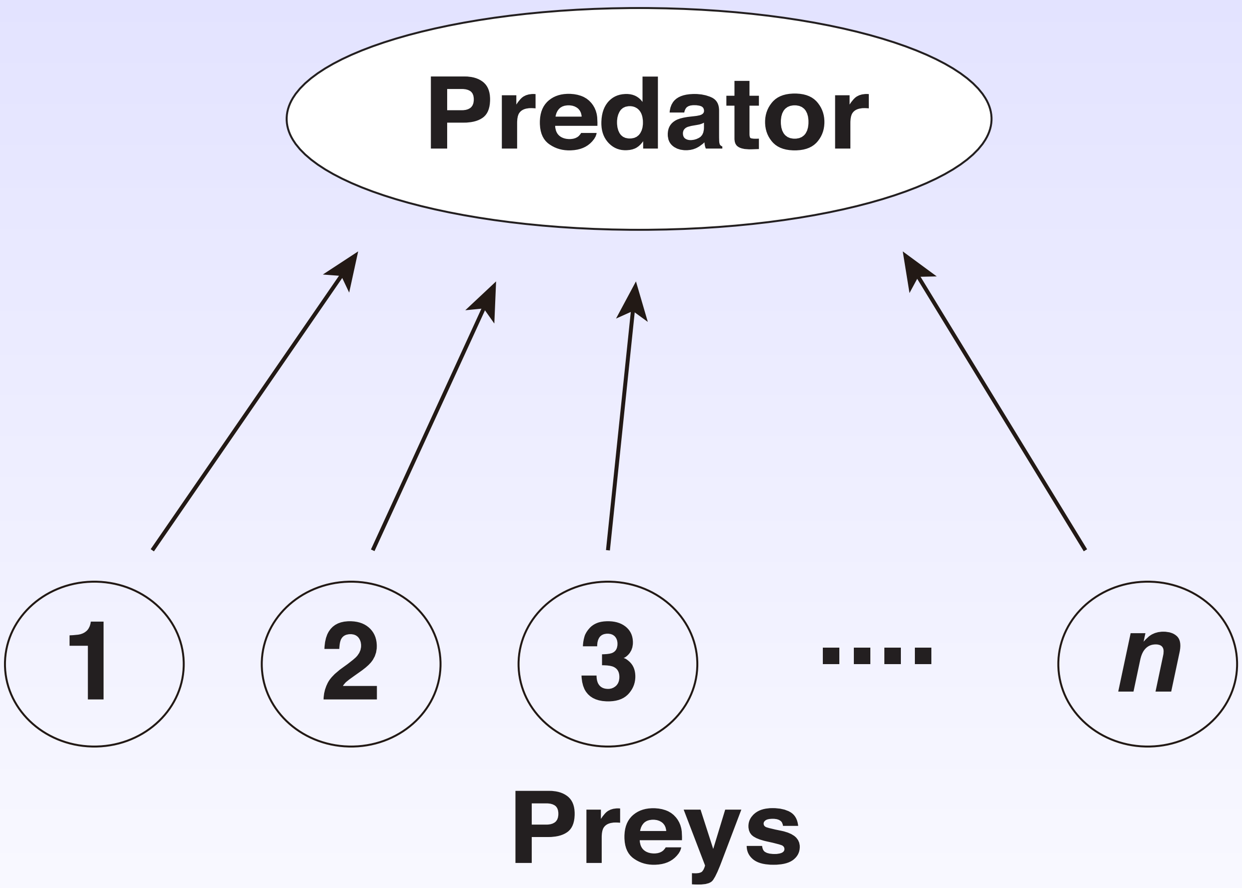
To suppress the pest resurgence, it is necessary to carefully plan the pest-harvesting operation, taking account of its timing and strength, after the necessary ecological assessment especially about the effectiveness of natural enemies.

Mathematical Model for Harvesting/Thinning

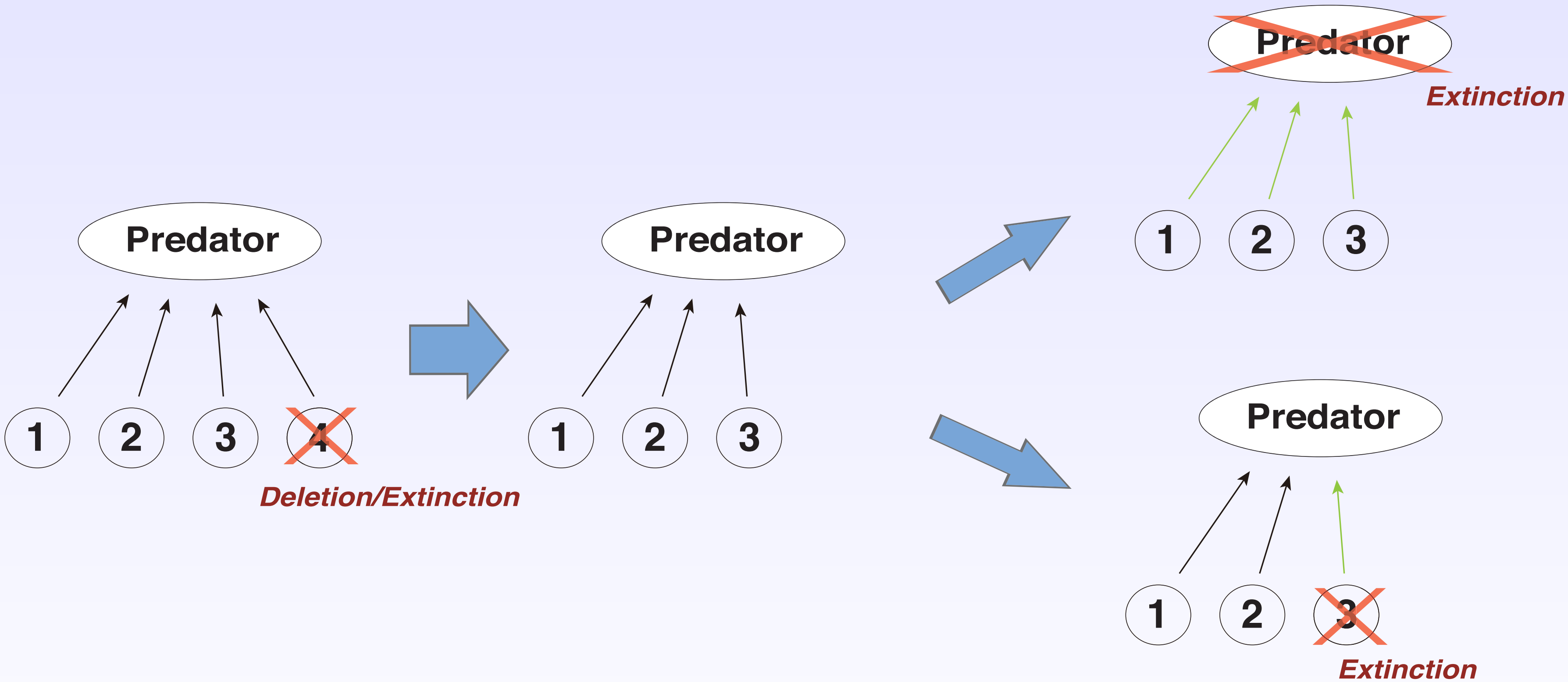
From the other viewpoint:

Harvesting/Thinning may be utilized to increase or sustain a population as an operation for its control.

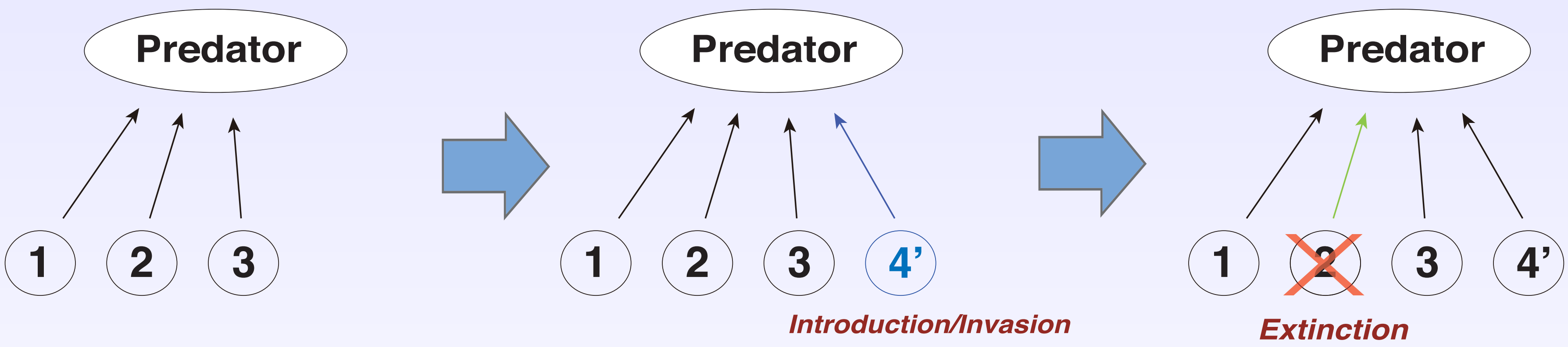
└Species Deletion/Introduction



Species deletion



Species introduction



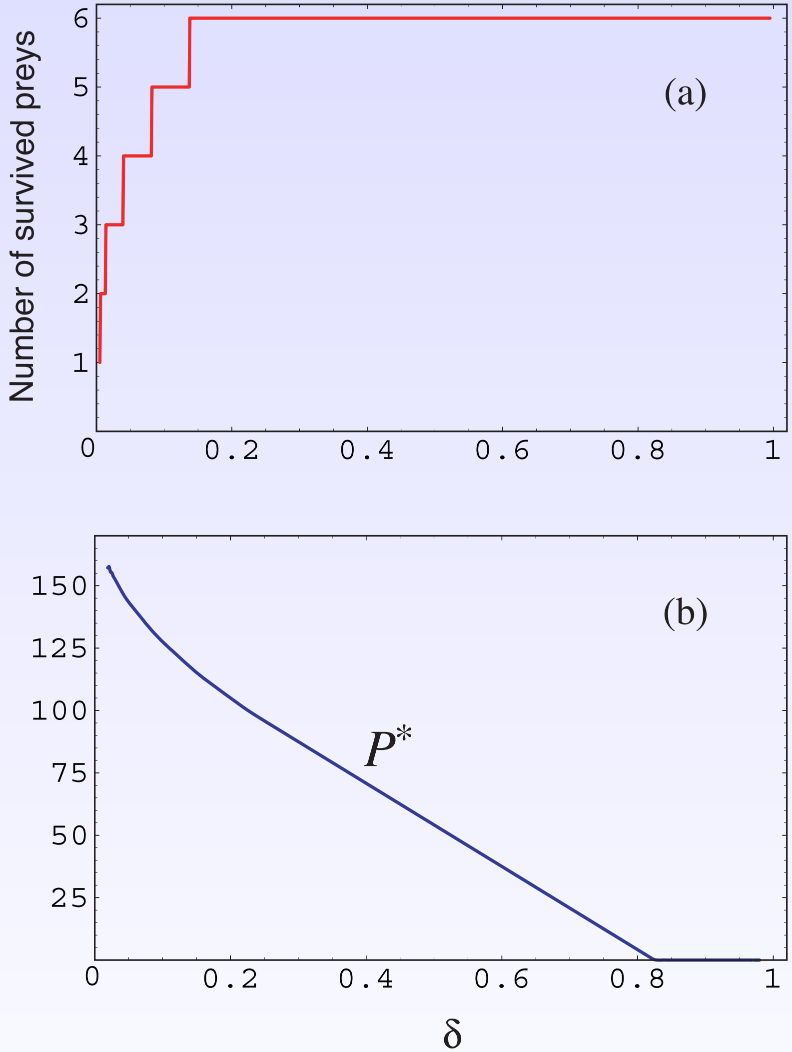
└Species Deletion/Introduction

Lotka–Volterra model for predator–prey system

$$\frac{dP}{dt} = -\delta P + \sum_{i=1}^{n} c_i b_i H_i P$$

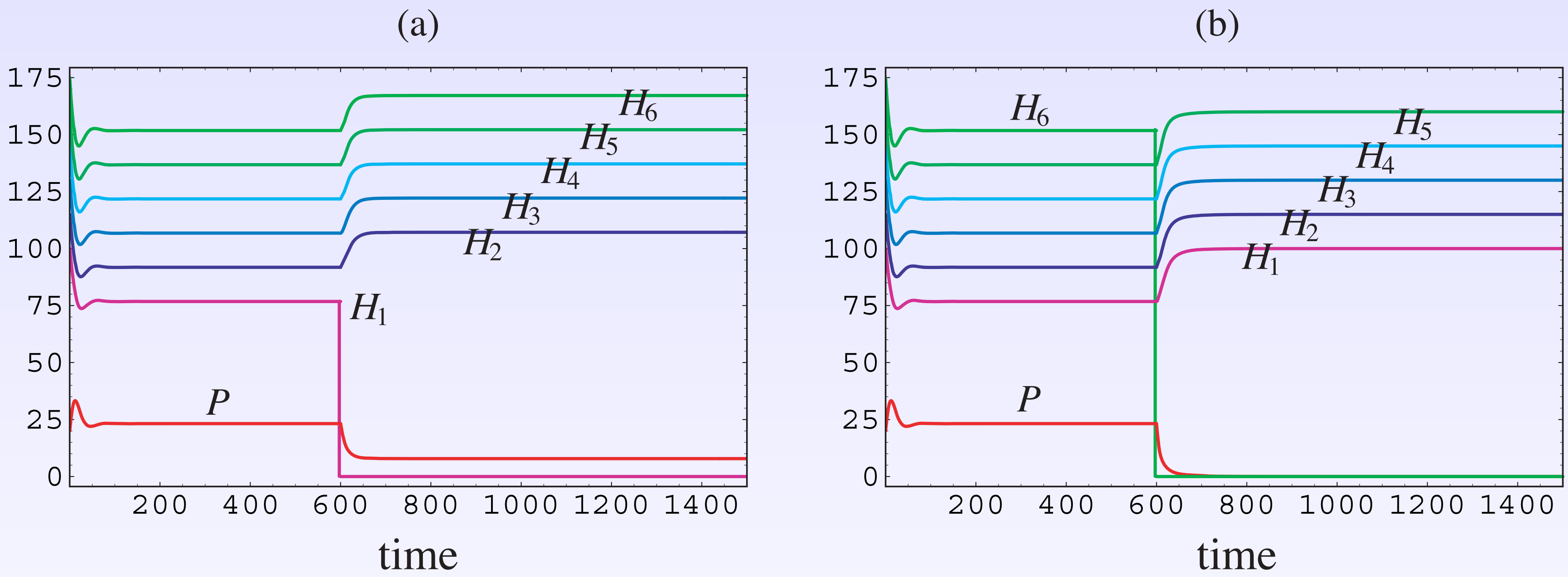
$$\frac{dH_i}{dt} = (r_i - \beta_i H_i) H_i - b_i H_i P \quad (i = 1, 2, \ldots, n)$$

└Species Deletion/Introduction



δ-dependence of the equilibrium state after a shared predator's invasion into the system with coexisting six prey species. (a) Number of survived prey species; (b) Equilibrium size of the predator population. $c_i = 0.1$; $r_1 = 0.1$; $r_2 = 0.115$; $r_3 = 0.13$; $r_4 = 0.145$; $r_5 = 0.16$; $r_6 = 0.175$; $b_i = 0.001$; $\beta_i = 0.0001\ (1 \leq i \leq 6)$.

Deletion of a prey species



Temporal variation of population sizes after the deletion of a prey species at $t = 600$ from the coexistent equilibrium state with a shared predator and six preys. (a) Prey H_1 is deleted. No secondary extinction occurs; (b) Prey H_6 is deleted. The shared predator goes extinct after the deletion. $P(0) = 20.0$; $H_1(0) = 100.0$; $H_2(0) = 115.0$; $H_3(0) = 130.0$; $H_4(0) = 145.0$; $H_5(0) = 160.0$; $H_6(0) = 175.0$; $\delta = 0.48$; $c_i = 0.7$; $r_1 = 0.1$; $r_2 = 0.115$; $r_3 = 0.130$; $r_4 = 0.145$; $r_5 = 0.16$; $r_6 = 0.175$; $b_i = 0.001$; $\beta_i = 0.001\ (1 \leq i \leq 6)$.

Predator population size after a native prey deletion

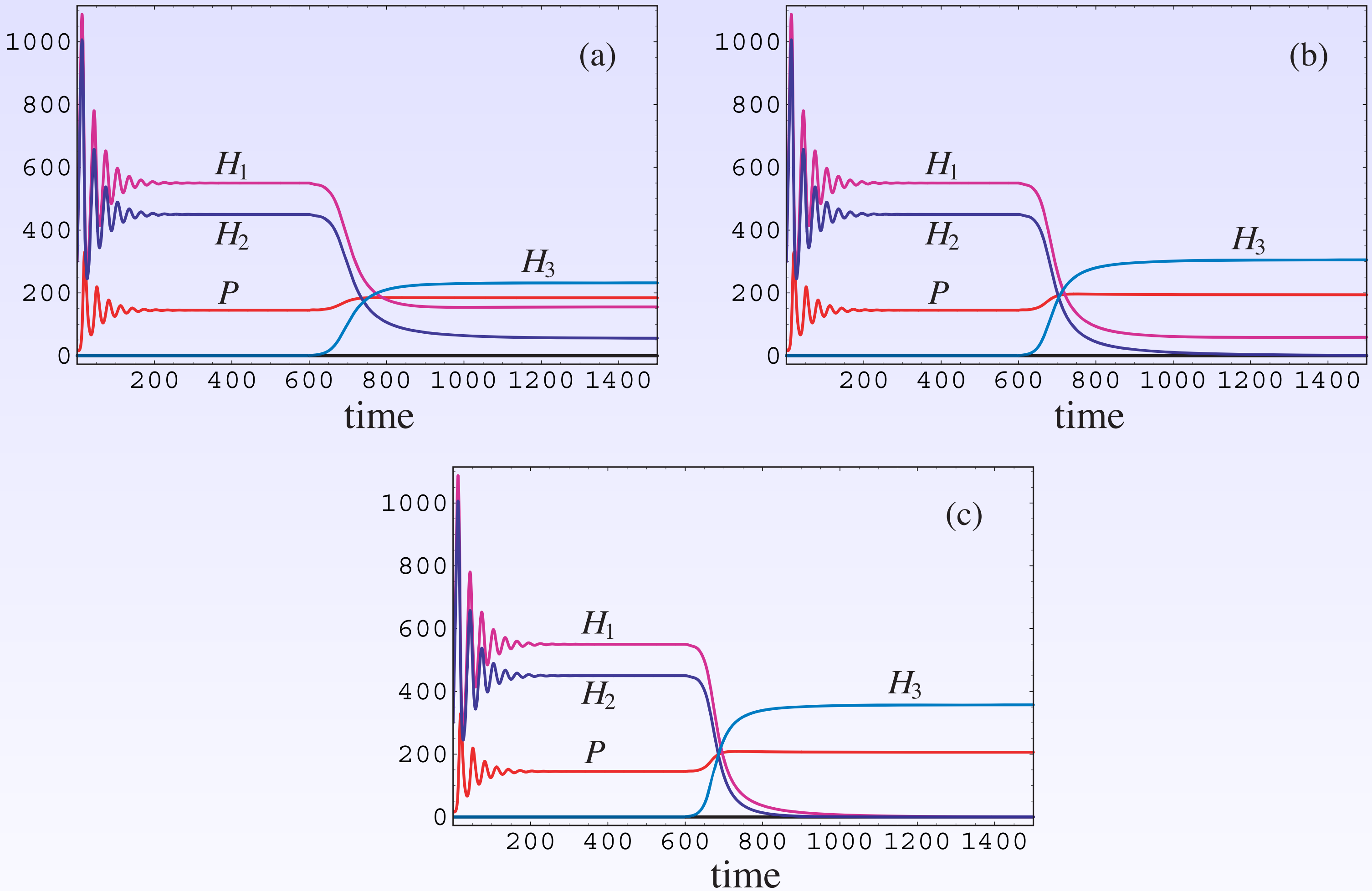
If a prey species is deleted *from the coexistent equilibrium state*, the system alternatively transits to the state at which the predator coexists with the whole rest of prey species or the state at which only the predator goes extinct.

Species Deletion/Introduction

Predator population size after a native prey deletion

By the deletion of a prey species *from the co-existent equilibrium state*, the system transits to an equilibrium state at which the predator population necessarily has a size smaller than before.

Introduction of an alien prey species



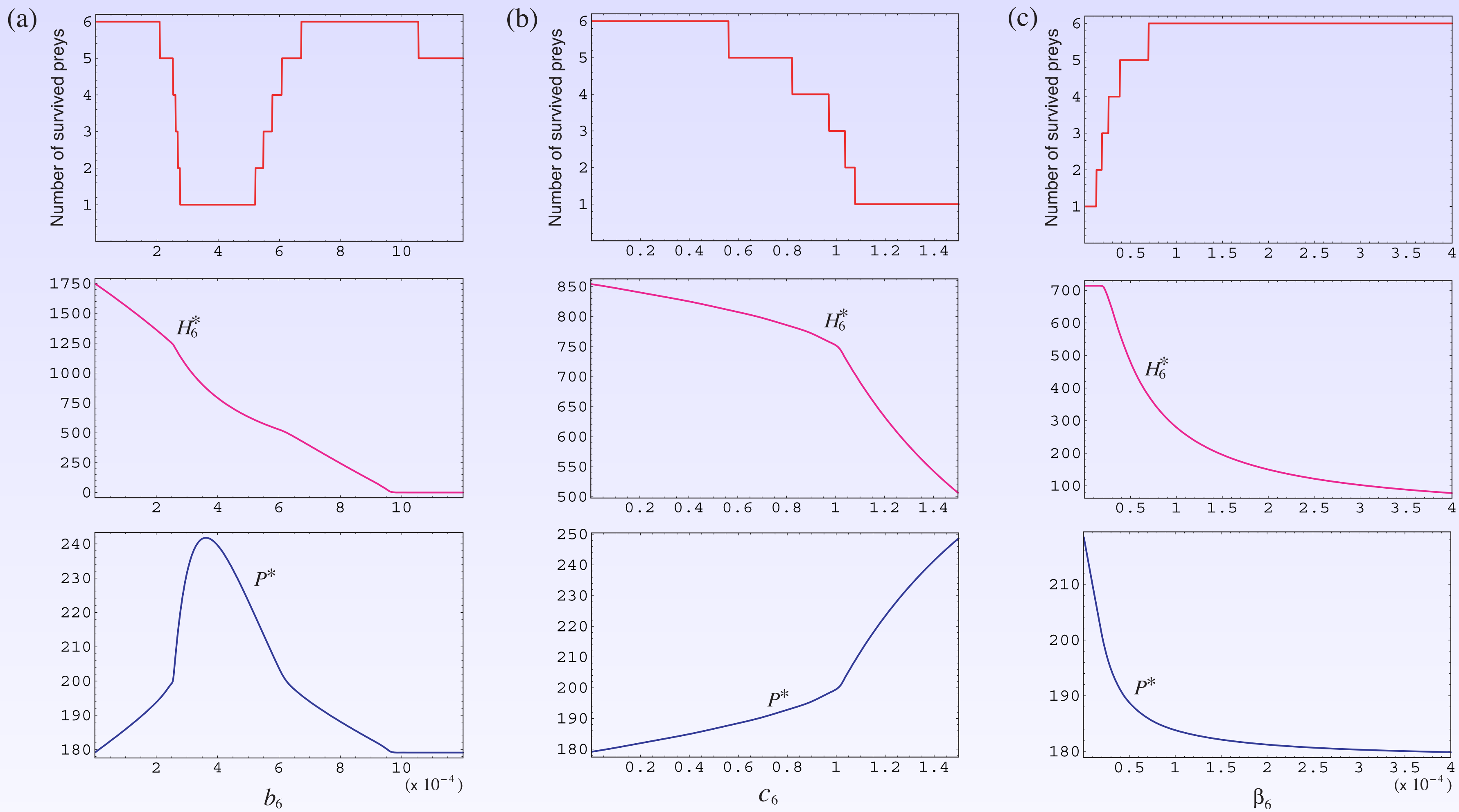
Temporal variation of population sizes after the introduction of prey H_3 at $t = 600$ into the coexistent equilibrium state with the shared predator and two preys. (a) $b_3 = 0.00085$. No extinction occurs. (b) $b_3 = 0.00077$. Prey H_2 goes extinct. (c) $b_3 = 0.0007$. Prey H_1 and H_2 go extinct. Commonly, $P(0) = 20.0$; $H_1(0) = 300.0$; $H_2(0) = 300.0$; $H_3(600) = 1.0$; $\delta = 0.3$; $c_1 = c_2 = 0.3$; $c_3 = 1.2$; $r_1 = 0.2$; $r_2 = 0.19$; $r_3 = 0.18$; $b_1 = b_2 = 0.001$; $\beta_1 = \beta_2 = \beta_3 = 0.0001$.

└Species Deletion/Introduction

Predator population size after alien prey introduction

If the system transits to a new equilibrium state without any extinction after the introduction of an alien prey species in the coexistent equilibrium state, the predator population has a size greater than before at the new coexistent equilibrium state.

└Species Deletion/Introduction



Parameter dependence of the equilibrium state after the introduction of prey H_6 into the system at the coexistent equilibrium state with a predator and five preys. Numerical calculations for the number of survived preys, the equilibrium size of the introduced prey H_6, and that of the shared predator population. (a) b_6-dependence with $(c_6, \beta_6) = (1.2, 0.0001)$; (b) c_6-dependence with $(b_6, \beta_6) = (0.0005, 0.0001)$; (c) β_6-dependence with $(c_6, b_6) = (0.7, 0.0008)$. Commonly, $\delta = 0.38$; $c_i = 0.7\ (1 \leq i \leq 5)$; $r_1 = 0.2$; $r_2 = 0.195$; $r_3 = 0.19$; $r_4 = 0.185$; $r_5 = 0.180$; $r_6 = 0.175$; $b_i = 0.001\ (1 \leq i \leq 5)$; $\beta_i = 0.0001\ (1 \leq i \leq 5)$.

└Species Deletion/Introduction

Predator population size after alien prey introduction

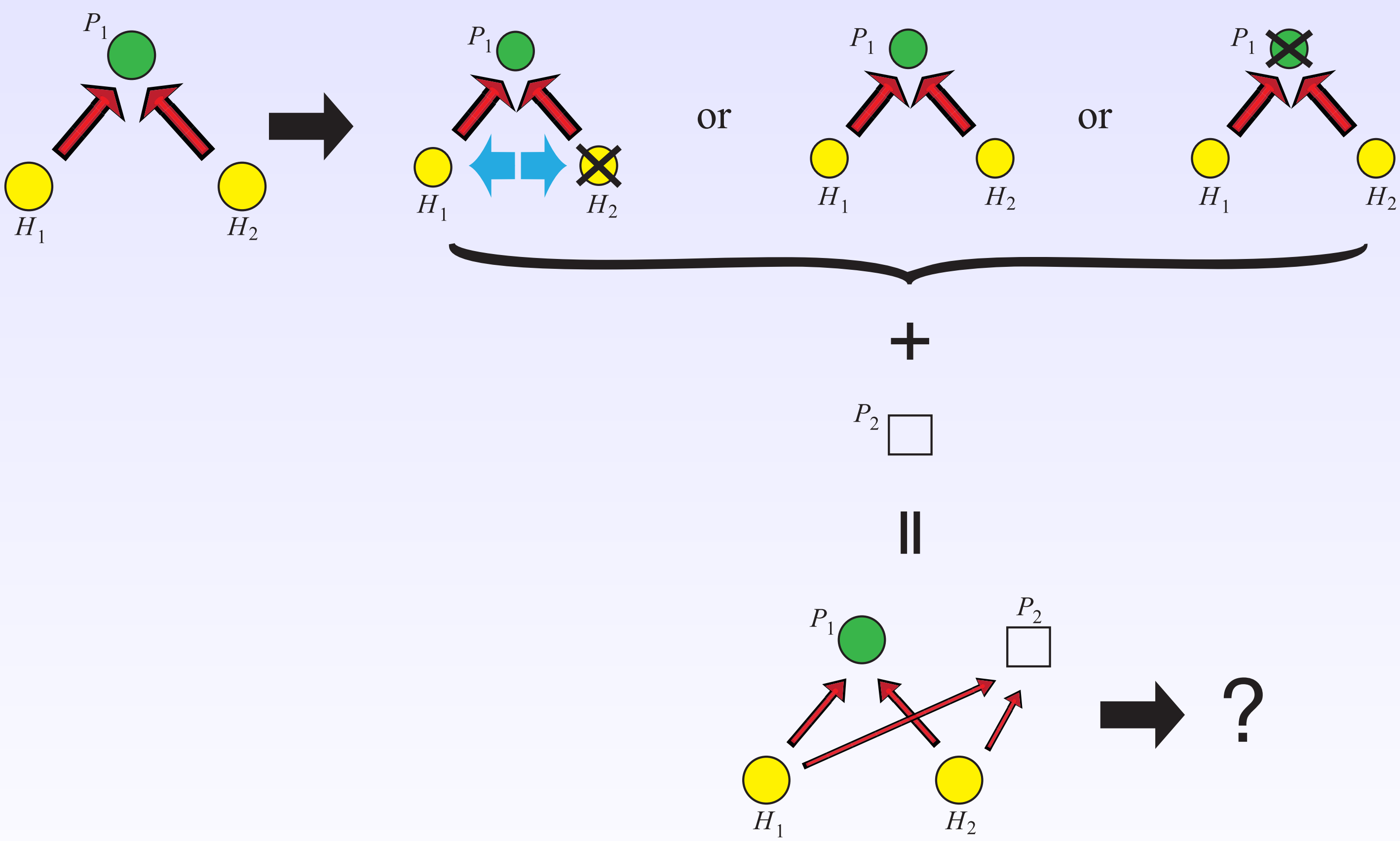
If the system transits to a new equilibrium state without the extinction of the introduced prey and the predator, the predator population is larger as the number of survived preys gets smaller at the new coexistent equilibrium state.

└Species Deletion/Introduction

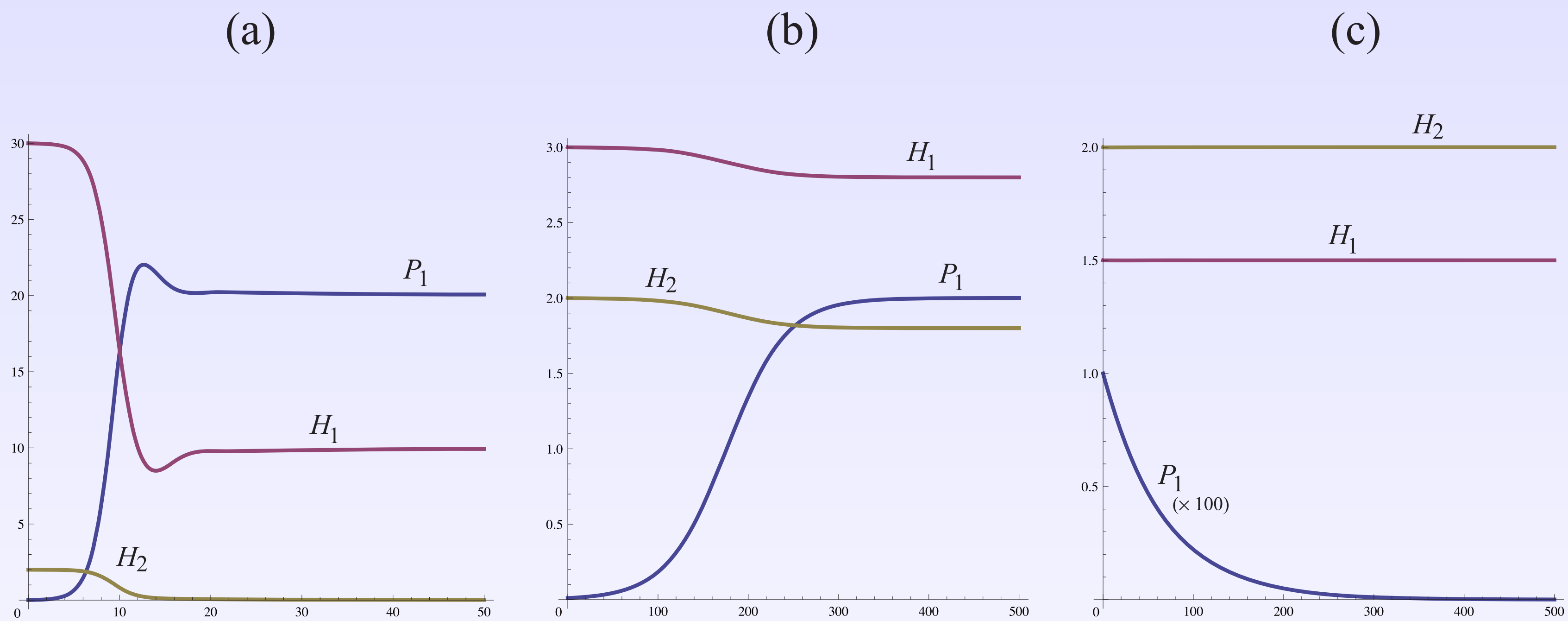
Native predator–prey system after an alien prey introduction

To increase/sustain the population size of native predator, introduction of an alien prey may be effective, although some native prey species could be subsequently threatened to go extinct.

1 predator– 2 prey system + alien predator



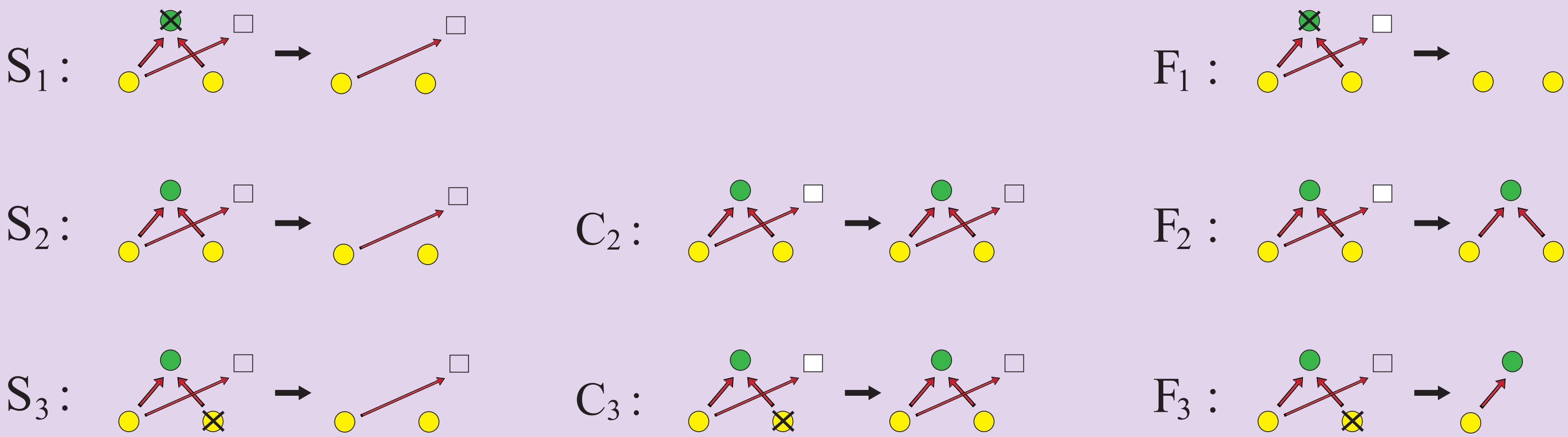
└Species Deletion/Introduction



Temporal variation of population sizes in Lotka–Volterra 1 predator– 2 prey system. (a) Extinction of prey 2 due to the apparent competition effect; (b) Coexistence of two preys and predator; (c) Extinction of predator. (a) $\beta_1 = 0.1$, $(P_1(0), H_1(0), H_2(0)) = (0.01, 30.0, 2.0)$; (b) $\beta_1 = 1.0$, $(P_1(0), H_1(0), H_2(0)) = (0.01, 3.0, 2.0)$; (c) $\beta_1 = 2.0$, $(P_1(0), H_1(0), H_2(0)) = (0.01, 1.5, 2.0)$. $\delta_1 = 0.3$, $b_{11} = 0.1$, $b_{21} = 0.1$, $c_{11} = 0.3$, $c_{12} = 1.2$, $\beta_2 = 1.0$, $r_1 = 3.0$, $r_2 = 2.0$. Initial value $H_i(0)$ equals to the carrying capacity r_i/β_i $(i = 1, 2)$.

Species Deletion/Introduction

Native predator–prey system after an alien predator introduction



Native predator–prey system after an alien predator introduction

In 1 predator– 2 prey system with native predator's going extinct, introduction of an alien predator cannot save the native predator from its extinction.

└Species Deletion/Introduction

Native predator–prey system after an alien predator introduction

In 1 predator– 2 prey system with native prey 2's going extinct, introduction of an alien predator which is specialist for prey 2 cannot save the native prey 2 from its extinction.

└Species Deletion/Introduction

Native predator–prey system after an alien predator introduction

In 1 predator– 2 prey system with native prey 2's going extinct, introduction of an alien predator which is specialist for prey 1 can lead the system to the coexistence of native preys and predator.

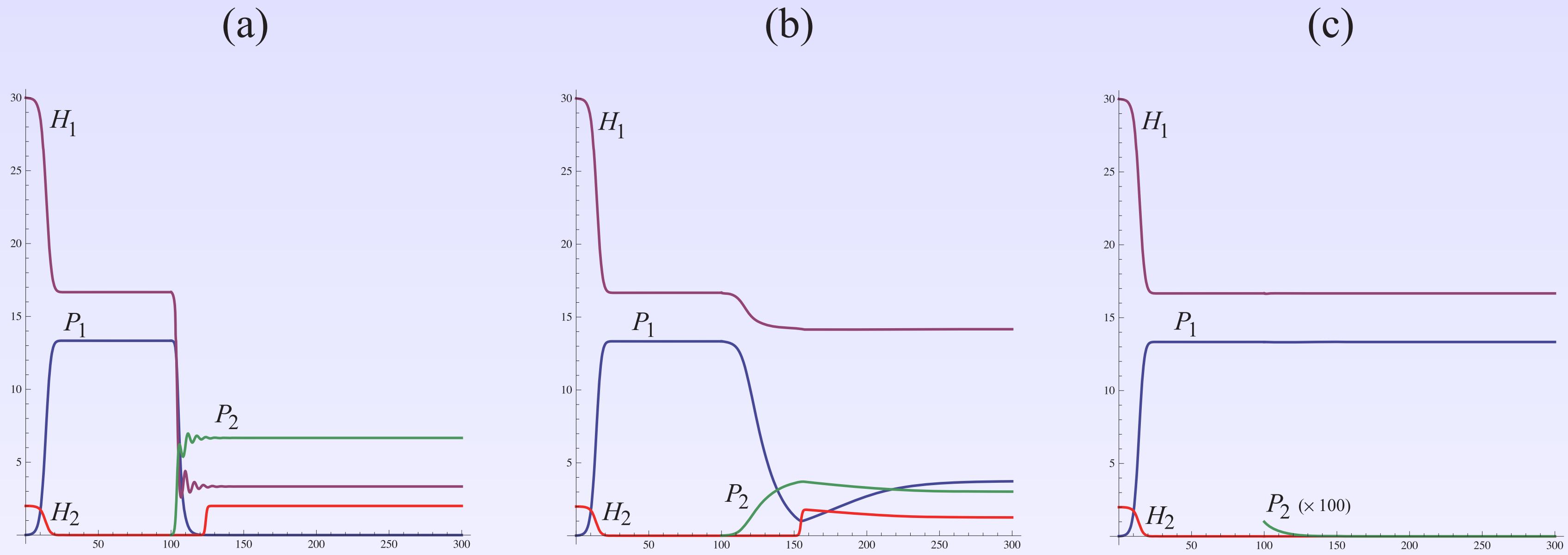
└Species Deletion/Introduction

Native predator–prey system after an alien predator introduction

In 1 predator– 2 prey system with native prey 2's going extinct, introduction of an alien predator which is specialist for prey 1 can lead the system to the coexistence of native preys and predator.

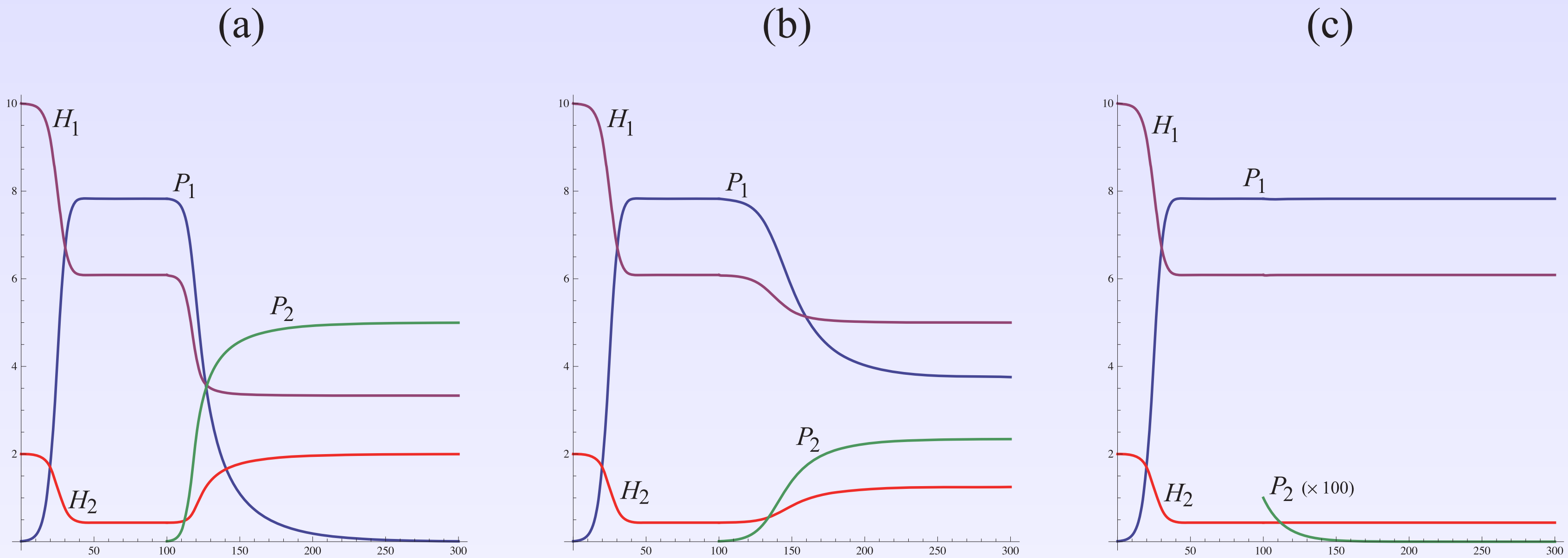
To save the native prey 2 from its extinction, prey 1 is to be predated in sufficiently high efficiency and to lead sufficiently large reproduction rate for the introduced alien predator.

└ Species Deletion/Introduction



Temporal variation of population sizes in Lotka–Volterra 1 predator– 2 prey system with prey 2's going extinct. An alien predator is introduced at $t = 100.0$. The alien predator is specialist for prey 1. (a) Prey 2 is saved from its extinction, while the native predator goes extinct. The system transits to the state with the alien predator and two native preys (the case of exploitative competition for predators, $\mathbf{S}_3$); (b) Preys is saved from its extinction, and the alien predator is settled to make the system transit to the state of coexistence of four species (the case of modification of apparent competition, $\mathbf{C}_3$); (c) Failure of alien predator introduction, and the extinction of prey 2 ($\mathbf{F}_3$). (a) $\delta_2 = 0.4$; (b) $\delta_2 = 1.7$; (c) $\delta_2 = 2.1$. $\delta_1 = 0.5$, $b_{11} = 0.1$, $b_{12} = 0.4$, $b_{21} = 0.2$, $c_{11} = 0.3$, $c_{12} = 0.3$, $c_{21} = 0.3$, $\beta_1 = 0.1$, $\beta_2 = 1.0$, $r_1 = 3.0$, $r_2 = 2.0$, $(P_1(0), H_1(0), H_2(0)) = (0.01, r_1/\beta_1, r_2/\beta_2)$, $P_2(100.0) = 0.01$. Initial value $H_i(0)$ equals to the carrying capacity r_i/β_i $(i = 1, 2)$.

└Species Deletion/Introduction



Temporal variation of population sizes in Lotka–Volterra 1 predator– 2 prey system with their coexistence. An alien predator is introduced at $t = 100.0$. The alien predator is specialist for prey 1. (a) Introduction of alien predator causes the extinction of native predator. The system transits to the state with the alien predator and two native preys (the case of exploitative competition for predators, $\mathbf{S_2}$); (b) Alien predator is settled to make the system transit to the state of coexistence of four species ($\mathbf{C_2}$); (c) Failure of alien predator introduction ($\mathbf{F_2}$). (a) $\delta_2 = 0.4$; (b) $\delta_2 = 0.6$; (c) $\delta_2 = 0.8$。 $\delta_1 = 0.3$, $b_{11} = 0.15$, $b_{12} = 0.4$, $b_{21} = 0.2$, $c_{11} = 0.3$, $c_{12} = 0.3$, $c_{21} = 0.3$, $\beta_1 = 0.3$, $\beta_2 = 1.0$, $r_1 = 3.0$, $r_2 = 2.0$, $(P_1(0), H_1(0), H_2(0)) = (0.01, r_1/\beta_1, r_2/\beta_2)$, $P_2(100.0) = 0.01$。 Initial value $H_i(0)$ equals to the carrying capacity r_i/β_i $(i = 1, 2)$.

Concluding Remarks

To maintain the ecological system and sustain the ecological service for human being, it is necessary to plan some operation for the ecological system ordinarily affected by human activity.

Not only to **conserve** it, but also to **control** it, we need to systematically discuss what and how an operation affects the target ecological system.

Thank you for your attention!

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