Population dynamics of Müllerian mimicry under interspecific competition

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ABSTRACT

We ask what the effects of mutualism on population dynamics of two competitive species are. We model the population dynamics of mutualistic interactions with positive density and frequency dependences. We specifically assume the dynamics of Müllerian mimicry in butterflies, where the mortality of both species is reduced depending on the relative frequency of the other species. We assume that the two species are under Lotka-Volterra density-dependent competition. The equilibria are compared with the cases of competition alone. Unlike the traditional model of positive density dependence, population explosion does not appear in the current dynamics, but the new equilibrium is simply achieved. It is because the effects of positive density or frequency dependence are restricted to parts of mortality. Both positive density and frequency dependences do promote coexistence of the mimetic species. However, the two models show a distinctive difference for coexistence. The effects of positive density dependence are rather limited. In contrast, positive frequency dependence always promotes coexistence, irrespective of environmental conditions. The results may imply that the evolutionary origin of Müllerian mimicry may depend on frequency dependence (and density dependence), but that its current population dynamics may depend solely on density dependence. The role of frequency and density dependences on evolutionary dynamics is an open question.

1. INTRODUCTION

Mutualism or symbiosis is often considered as one of the major categories of ecological interactions of populations or species (McNaughton and Wolf, 1979; Begon et al., 1996). Recently, mutualism is also suggested as an important factor of community stability in general (Golick et al., 1978; May 1982; Pellmyr and Huth, 1994). However, the population dynamics of mutualistic relations are rarely described, except the case of positive density dependence (May 1982; Bertness and Hacker, 1994, 1997; Stiling, 1999). The population equation with positive density dependence is in contrast with the negative density dependence of Lotka-Volterra type competition (May, 1976; Ginzburg, 1983; Boucher, 1985; Tainaka et al., 2003). However, positive density dependence is problematic, since strong mutualism leads to the infinite population growth or population explosion (May, 1982; Tainaka et al., 2003).

Here we consider the population dynamics of mutualistic interactions. One such example is the dynamics of Müllerian mimicry in butterflies, in which the benefits of mimicry are mutual between the two toxic butterfly species. Müllerian mimicry is one of famous example of symbiotic relationships (Wicker, 1968). Its evolutionary mechanisms have been studied extensively (Futuyma and Slatkin, 1983). However, the population processes of such mutualistic relationships are not well understood.

Recently frequency dependence has been discussed as a new type of population interactions in the dynamics of competition (Kuno, 1992; Yoshimura and Clark, 1994) and predation (Hori, 1993; Takahashi and Hori, 1994). The known dynamics of frequency dependence are strikingly different from the traditional population dynamics, in which density dependence is the regulatory factor. Positive frequency dependence is applicable to Batesian mimicry (Wickler 1968), because the frequency of the noxious model is a critical factor in the predatory escape of the mimic (Kumazawa et al., 2006). In contrast, Müllerian mimicry is the case, where positive density and/or frequency dependence are expected.

This paper describes the basic population dynamics of positive density and frequency dependences. We assume that the mortality of both species is reduced depending on the density or relative frequency of the other species. We also assume that the two species are under density-dependent competition. These processes may describe some features of Müllerian mimicry and other mutualistic relationships.

We analyze the equilibria using phase planes. The equilibria are then compared with the case ~~of~~ Lotka-Volterra type competition alone. Both positive density and frequency dependence promote the coexistence of different mimics. However the former is rather limited in its effect. In either case, the dynamics leads to a new equilibrium without any population explosion.

2. MODEL OF POSITIVE DENSITY AND FREQUENCY DEPENDENCES

2.1. Reduction in mortality

In Müllerian mimicry both a mimic and its model are poisonous or unpalatable. Müllerian mimicry in poisonous butterflies is known to reduce the mortalit~~y~~ies of both the mimic and model (Wickler, 1968). ~~Experienced~~ By experiencing the noxious taste, birds learn the wing patterns of poisonous or unpalatable butterflies and avoid catching them. However naïve (inexperienced) birds with almost no learning experience tend to prey on these poisonous butterflies. Therefore, butterflies are eaten by naïve birds until ~~the birds learn~~ their wing patterns are learned.

If there are two poisonous butterflies similar in wing patterns, their predation rates are reduced by enhancing the learning experience of naïve birds. If birds does ~~can~~not recognize ~~the~~ differences in the~~ir~~ wing patterns of butterflies, birds ~~predate~~ prey and learn them as a single type of non-palatable butterflies~~species~~. Therefore, the mortality of each butterfly species is reduced depending on the total density of both species. Suppose two

sympatric species S_i (i =1,2). The reduction rate in predatory mortality, d_i, should depend on the total density:

$$d_i \;=\; d_i\,(N_1 + N_2) \;=\; 1/(N_1 + N_2), \quad i=1,2. \qquad (1)$$

where N_i is the population size of species i. Here we assume $N_1 + N_2 \geq 1$, so that $d_i \leq 1$. Note that $d_i = 1$ indicates no reduction in mortality, whereas $d_i = 0$ is a 100% reduction in mortality.

In contrast, symbiosis may be ~~more like~~ frequency-~~-~~dependent~~ee~~. The existence of symbionts may enhance ~~the~~ population growth ~~of~~ in a species by increasing the survival of ~~the~~ individuals. We would expect ~~the~~ mutualistic benefits in such symbiosis, e.g.~~,~~ ~~that~~ between lycaenid butterfly and ants, ~~that between~~ hermit crabs and sea anemones, ~~and~~ or ~~lichen (symbiosis between~~ fungi and algae~~)~~ in lichens. In symbiosis, the existence of the other species reduces the cost/mortality of the symbionts. Then the relative frequency f_i of a species is an appropriate measure of mortality reduction, such that:

$$f_i \;=\; f_i\,(N_1, N_2) \;=\; N_i/(N_1 + N_2), \quad i=1,2. \qquad (2)$$

Here f_i indicates that the existence and population size of the mutualistic partner enhances the reduction of mortality. With no partner, $f_i = 1$ (no reduction) and with infinite partners, $f_i = 0$ (the 100 % reduction in mortality).

We should note that the density-dependent reduction ~~in~~ of mortality might be applicable to Müllerian mimicry. However, ~~the~~its frequency-dependent reduction cannot be applicable, because both the mimics and models gain benefits of other individuals irrespective of species. Thus, the frequency-dependent equation (Eq. 2) should not be applicable to the mutualism apparent in Müllerian mimicry.

The partial mortality of each species may be reduced depending on the total

density or ~~the~~ relative frequency of the other species. It is natural that such <u>a</u> reduction is limited to a certain kind of mortality, e.g.~~,~~ <u>by</u> bird predation in Müllerian mimicry. These functions may be complex, but for simplicity we assume that the reduction rate of a species $h_i = d_i$ ~~−~~ or f_i (Equations 1 and 2).

2.2. Population dynamics equation

To evaluate <u>the</u> mortality separately from <u>the</u> birth rates, the population growth rate r_i is separated into <u>the</u> birth and mortality rate<u>s</u>. Let $b_i = b_i(N_i, N_j, a_{ij})$ and $\hat{m}_i = \hat{m}_i(N_i, N_j, \alpha_{ij})$ denote the birth ~~rate~~ and mortality rate<u>s</u>, respectively (Fig. 1). Note that the term $\hat{m}_i$ includes the reduction of mortality incurred by mutualistic interactions. The population dynamic equations are then expressed as

$$\frac{dN_i}{dt} = (b_i - \hat{m}_i)N_i \qquad \text{——} \qquad \underline{\qquad\qquad} \qquad (3)$$

The terms b_i and $\hat{m}_i$ are defined as

$$b_i = b_{ik} + (b_{i0} - b_{ik})\left(1 - \frac{N_i + \alpha_{ij}N_j}{K_i}\right) \qquad (4)$$

$$\hat{m}_i = (1 - p_{i1})m_{i0} + (1 - p_{i2})(m_{ik} - m_{i0})\left(\frac{N_i + \alpha_{ij}N_j}{K_i}\right)$$

$$+ h_i\left\{p_{i1}m_{i0} + p_{i2}(m_{ik} - m_{i0})\left(\frac{N_i + \alpha_{ij}N_j}{K_i}\right)\right\} \quad (5)$$

where p_{i1} and p_{i2} are the density-independent <u>mortality</u> and density-dependent fraction~~s~~ of ~~reduced~~ mortality <u>reduction</u>, respectively. The other parameters are as follows. The terms b_{i0} and m_{i0} denote the intrinsic birth and death rates, respectively<u>,</u> and $b_{ik} = m_{ik}$ denote the birth and death rates at the carrying capacity $N_i = K_i$. α_{ij}, is the Lotka-Volterra competition coefficient of species j on i. Note that $b_{i0} \geq b_{ik} = m_{ik} \geq m_{i0}$ (Fig. 1). If $h_i = 1$ and/or $p_{i1} = p_{i2} = 0$, Equation 2 collapses to the Lotka-Volterra competition equation with $r_i = b_i - m_i$, where $m_i = \hat{m}_i$ when $p_{i1} = p_{i2} = 0$.

3. RESULTS

Setting $dN_i / dt = 0$, we obtain the zero-growth isoclines for S_i, viz. $b_i \cdot \hat{m}_i = 0$ (Fig. 2). The isocline of positive density dependence is the straight line parallel to that of the Lotka-Volterra competition model (Fig. 2 A), because it is simply enlarged by the total density $N_1 + N_2$. Therefore, $z_d = K_d / \alpha_{12}$. In contrast, the isocline of frequency dependence is a concave curve originated from $N_1 = K_1$ (Fig. 2 B).

Some phase plains for positive density dependence are shown in Fig. 3. The relationships between species are identical to those of the Lotka-Volterra competition model, while the four intercepts are proportionally enlarged. Thus the equilibria ~~is~~ are qualitatively identical to those of the competition model. For the case of coexistence, the equilibrium densities of both species are increased proportionally (Fig. 3 A). Therefore, <u>the</u> coexistence is said to be quantitatively promoted. However, in the other three cases, the relationship is also enlarged. Therefore, <u>the</u> exclusion is said to be actually strengthened (one case is shown in Fig. 3 B).

The equilibrium cases for positive frequency dependence are shown in Fig. 4. Here coexistence is always promoted by the existence of the other species. Equilibrium states are qualitatively changed from exclusion to coexistence. Coexistence becomes possible if the effects are larger than a certain threshold (Fig. 4 A and B). If coexistence is maintained under competition, positive frequency dependence simply enlarges the equilibrium density, as in the case of coexistence with positive density dependence (Fig. 3 A). However, the stability is also increased by increasing the curvatures of the isoclines, unlike that of positive density dependence.

4. DISCUSSIONS

The current results show that mutualistic interactions do not invoke population explosion. The new equilibria are simply achieved in all cases. Mutualistic interactions usually affect some limited aspects of life history. In the current model, only partial mortality is reduced by mutualistic interactions. It is possible that the reproduction or birth rate may be increased to a certain limit. However, the effects of such interactions are always limited or restricted in some form or another. The lLattice model is another type of with such limitations (Tainaka et. al., 2003). Symbiotic relationships never invoke infinite population growth, because of limited effects on population growth.

Our results also show that the effects of positive density dependence are rather limited. When the environmental conditions of for the two species are different, positive density dependence may promote coexistence even if the coexistence is not achieved under Lotka-Volterra competition alone. However, when the environmental conditions for of the two species become identical, positive density dependence increases the equilibrium densities of both species, only if their coexistence has been already achieved (Fig. 3). This means that the ecological and life history traits of the two species are very similar. Here coexistence may not be promoted by positive density dependence. The equilibrium density is increased only when coexistence is achieved under Lotka-Volterra competition alone. Here positive density dependence does not promote coexistence, but stabilizes coexistence by enlarging the equilibrium densities. Thus the effects of positive density dependence are limited under a narrow range of the environmental (parameter) conditions.

In contrast, frequency dependence always promotes coexistence. When coexistence is not achieved under competition, positive density dependence always changes the species isoclines toward coexistence. When the two species already coexist under competition, coexistence is further stabilized. Thus positive frequency dependence promotes coexistence in any environmental condition.

Our analyses of population dynamics suggest the direction of evolution in

mutualitic interactions. For example, Müllerian mimicry may evolve when the mimic is not so similar to the model due to positive density/frequency dependences. However, when the mimic evolves to be almost identical to the model species, the mutualistic interactions only result in the stabilizing effect on coexistence due to the positive density effects. Note that frequency dependence should disappear, because predator~~y animal~~s cannot separate the model and the mimic at this stage. Density dependence should be always in effect in the evolutionary course of Müllerian mimicry. However, its strength is unknown and should be diminishing towards the completion of mimicry states, resulting only in stabilizing effects when coexistence is guaranteed without it (Fig. 3).

We do not know whether frequency dependence has a significant role in the evolution of Müllerian mimicry. Frequency dependence should be in effect for Batesian mimicry (Kumazawa et al. 2006). Therefore, it ~~should~~ could be in principle working in the early stage of Müllerian mimicry under ~~the same~~ a similar mechanism. We suspect that frequency dependence is important in the early stages of Müllerian mimicry, while density dependence takes places in the later stages.

In our models, we consider the rate of predation as a parameter. However, in reality, every year young naïve animals (birds and mammals) try to eat these ~~poisonous~~ distasteful butterflies. Once they try, they will learn that these butterflies are ~~inedible or~~ not good to eat. The number of such learning losses should be proportional to the population sizes of predator~~y animal~~s, but not related to the population sizes of these butterflies. Therefore, the mortality ~~loss~~ by predation should decrease significantly when the mimic ~~is not~~ becomes distinguishable from the model. Thus the mortality rate may vary dynamically ~~due to~~ depending on the number of naïve ~~animal~~predators. This effect may be represented by positive frequency dependence (Fig. 5).

The evolution of Müllerian mimicry may proceed further. Once the complete mimicry against predator is achieved, the ~~poisonous~~ strength of noxiousness may be lowered, because~~.~~ ~~P~~producing or processing poisons are often costly in insects. ~~Once~~

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avoidance learning by predators are in effects, the butterflies may reduce the amounts of poisons without decreasing the avoidance learning. Müllerian mimicry increases the population size of the poisonous butterflies from the predators' point of view, resulting in predators' effective avoidance learning of avoidance. In response, both the models and mimics may evolve to decrease the amount of poisons; inedible (poisonous) butterflies may evolve to be a distasteful butterfly.

Recently negative frequency dependence is proposed in competition (Kuno, 1992, Yoshimura and Clark 1994), predation (Stiling, 1999, e.g., Hori, 1993, Takahashi and Hori 1994) and Batesian mimicry (Kumazawa, 2006). In principle, positive frequency dependence seems valid in symbiotic relationships. However, the functional relationships of Müllerian mimicry indicate that positive frequency dependence is not applicable when it is fully in effect. It is an open question whether Müllerian mimicry is a special case of mutualism or not. In our original model, Lotka-Volterra competition is assumed. For example, in lichens, algae and fungi could be under competition for space because of the limited space for growth of cells. However, symbiosis may also evolve without interspecific competition between symbionts. In such cases, frequency dependence could be a powerful effect on the evolution of mutualistic relationships. Because community stability is enhanced by mutualistic interactions (Golick, Atkins and Losey, et al. 1978, May, 1982), many of the present natural communities may have evolved and are sustained by such mutualistic interactions.

There are many different types of mutualistic interactions within a complicated food web. Some may depend on the density of the other species; some on the frequency; and others may be the combination of both. We have to evaluate the functional response of individuals in natural communities to determine the population-level effects of such interactions. As Tainaka et al. (2003) suggested, mutualistic interactions may only be effective when the environmental conditions are good (in a certain range), but competition

arises under severe environmental conditions. Both mimicry and mutualistic interactions are unsolved topics in population dynamics and evolutionary studies of ecological interactions. The role of frequency and density dependences on evolutionary dynamics is an open question.—

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In our analysis, because of the nature of Müllerian mimicry we have to develop a modified version of the Lotka-Volterra model with density-dependent, and density independent mortalities (Fig. 1). The growth rate is the only growth parameter in the traditional Lotka-Volterra competition model and in many applications and developments of that model (Ginzburg, 1983; Moreira and Yuquan, 1997; Huang and Zu, 2001; Rocha Filho et al., 2005; Vandermeer, 2008; Fay and Greeff, 2008). The gGrowth rate is separated into the birth and death rates, or similar parameters in some applications (Yoshimura and Clark 1994), especially plant competition models (Svirezhev, 2000; Bampfylde, et al. 2005). In the acutual real biological systems, mortality factors are often either density-dependent or density-independent. By separating these factors, we may estimate the effects of these mortality factors correctly. Our approach also indicates that every birth and mortality factors, which are density-independent or -dependent, can be separated into a separate parameter (Fig. 1). Thus the current approach may provide a new development for these the applications and developments of interspecific competition models.

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REFERENCES

Bampfylde, C.J., Brown, N.D., Gavaghan, D.J., Maini, P.K., 2005. Modelling rain forest diversity: The role of competition. Ecological Modelling 188: 253-278.

Begon, M., Harper, J.L., Townsend, C.R., 1996. Ecology: Individuals, Populations and Communities. Blackwell Publishing, Oxford, 1068 pp.

Bertness, M. D., Hacker, S. D., 1994. Physical Stressand Positive Associations Among Marsh plants. American Naturalist. 144, 363-372.

Bertness, M.D., Leonard, G.H., 1997. The Role of Positive Interactions in Communities: Lessons from Intertidal Habitats. Ecology. 78, 1979-1989.

Boucher, D.H. (eds.), 1988. The Biology of Mutualism: Ecology and Evolution. Oxford University Press, Oxford, 400 pp.

Fay, T.H., Greeff, J.C., 2008. A three species competition model as a decision support tool. Ecological Modelling 211: 142-152.

Futuyma, D.J., M Slatkin (eds.), 1983. Coevolution. Sinauer Asocates Inc., Sunderland, 555 pp.

Ginzburg. L.R., 1983. Theory of natural selection and population growth. Benjamin/Cummings, Menlo Park, Ca.

Gorlick, D.L., Atkins, P.D., Losey, G.S., 1978. Cleaning Stations as Water Holes, Garbage Dumps, and Sites for the Evolution of Reciprocal Altruism. American Naturalist. 112, 341-353.

Hori, M., 1993. Frequency-Dependent Natural Selection in the Handedness of Scale-Eating Cichlid Fish. Science. 260, 216-219.

Huang, X., Zu, Y., 2001. The LES population model: essentials and relationship to the Lotka-Voltrra model. Ecological Modelling 143: 215-225.

Kumazawa, F., Asami, T., Hayashi, T., Yoshimura, J., 2006. Population dynamics of Batesian mimicry under interspecific competition. Evolutionary Ecology Research 8(4), 591-604.

Kuno. E., 1982. Competitive exclusion through reproductive interference. Researches on Population Ecology. 34, 275-284.

May. R.M.(eds.), 1976. Theoretical Ecology: Principles and Applications. In: May. R.M. (ed.), Models for two interacting populations. Saunders, Philadelphia, USA, pp. 49-70.

May. R.M., 1982. Mutualistic interactions among species. Nature. 296, 803-804.

McNaughton. S.J., Wolf. L.L., 1979. General ecology, second edtion. Holt, Rinehart and Winston, New York, 710 pp.

Moreira, H.N., Yuquan, W., 1997. Global stability in a class of competitive cubic systems. Ecological Modelling 102: 273-285.

Pellmyr. O., Huth. C.J., 1994. Evolutionary stability of mutualism between yuccas and yucca moths. Nature. 372, 257-260.

Rocha Fulho, T.M., Gléria, I.M., Figueiredo, A., Brenig, L., 2005. The Lotka-Volterra canonical format. Ecological Modelling 183: 95-106.

Stiling. P., 1999. Ecology: Theories and Applications, third edition. Prentice Hall International, London, 638 pp.

Svirezhev, Y., 2000. Lotka-Volterra models with the global vegetation pattern. Ecological Modelling 135: 135-146.

Tainaka. K., Yoshida. N., Terazawa. N., Nakagiri. N., Takeuchi. Y., Yoshimura. J., 2003. The Effect of Mutualism on Community Stability. Journal of the Physical Society of Japan. 72(4), 956-961.

Takahashi. S., Hori. M., 1994. Unstable Evolutionarily Stable Strategy and Oscillation: A model of Lateral Asymmetry in Scale-Eating Cichlids. American Naturalist. 144, 1001-1020.

Vandermeer, J., 19972008. The niche construction paradigm in ecological time. Ecological Modelling 214: 385-390.

Wickler. W., 1968. Mimicry in Plants and Animals, McGraw-Hill, New York, 253 pp. (English translation, reprint: 1974).

Yoshimura. J., Clark. C.W., 1994. Population dynamics of sexual and resource competition. Theoretical
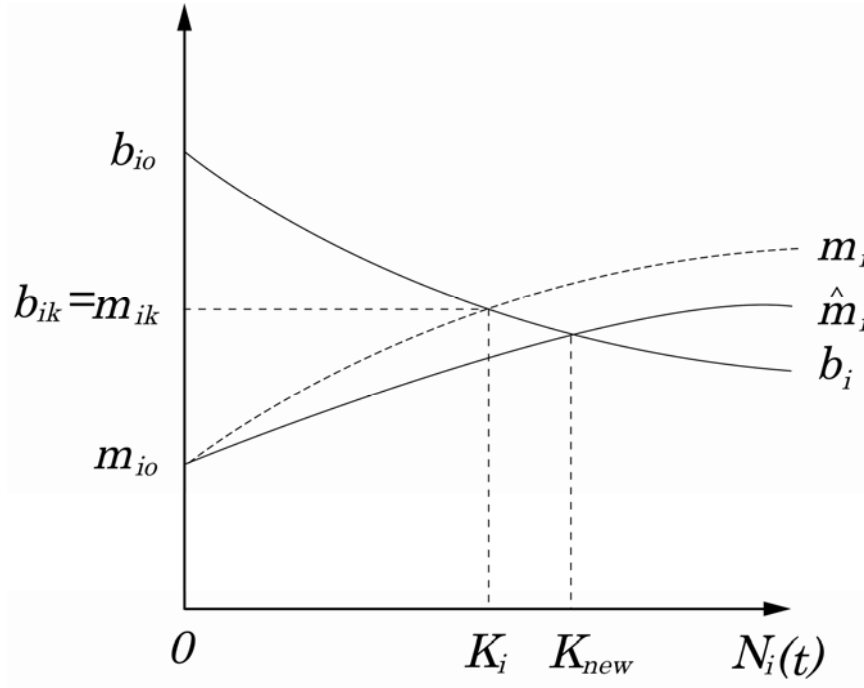
    Population Biology. 45, 121-131.

Fig. 1 - The schematic relationships among the birth rate b_i and mortality rate $\hat{m}_i$. Both b_i and $\hat{m}_i$ are the functions of the current population size $N_i(t)$ (Equations 4 and 5). The actual mortality $\hat{m}_i$ (dotted line) is lower than the mortality without mutualism m_i. Density dependent balance between mortality and birth rates at $N_i = K_i$ moves to the intersection between the solid mortality line $\hat{m}_i$ and the solid birth line b_i ($N_i = K_{new}$).
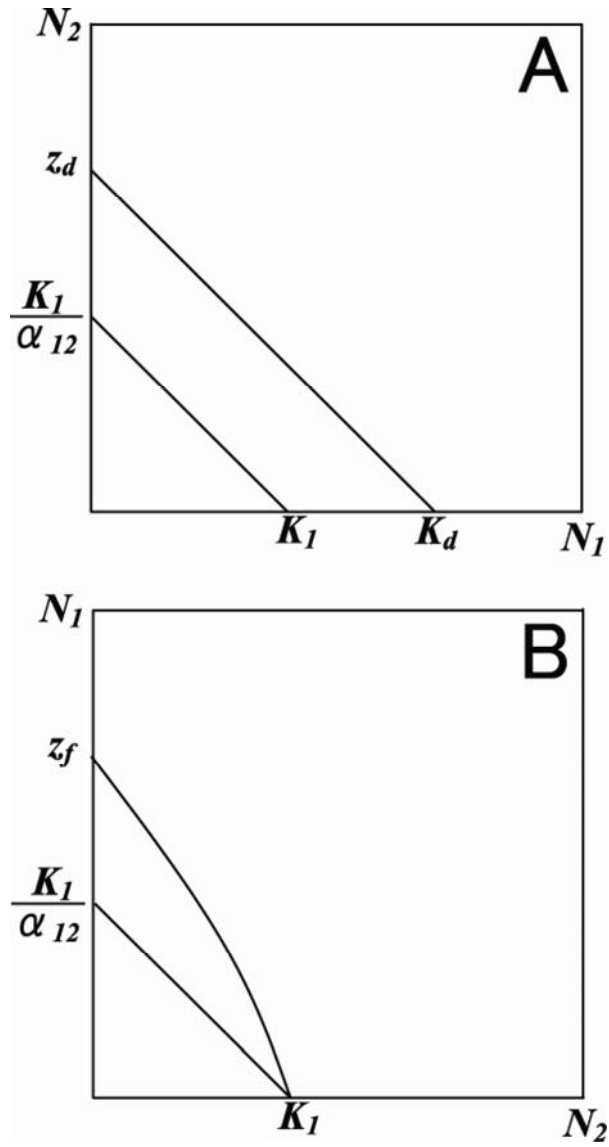
Fig. 2 - Isoclines for the population dynamics of positive density and frequency dependences. The isoclines of Lotka-Volterra competition model are also shown for comparison. (A) positive density dependence: the N_1- and N_2-intercepts are K_d and z_d, respectively. (B) positive frequency dependence: the N_1- and N_2-intercepts are K_1 and z_f, respectively.   Both z_d and z_f are larger than K_1/α_{12}, the N_2-intercept of the competition model.
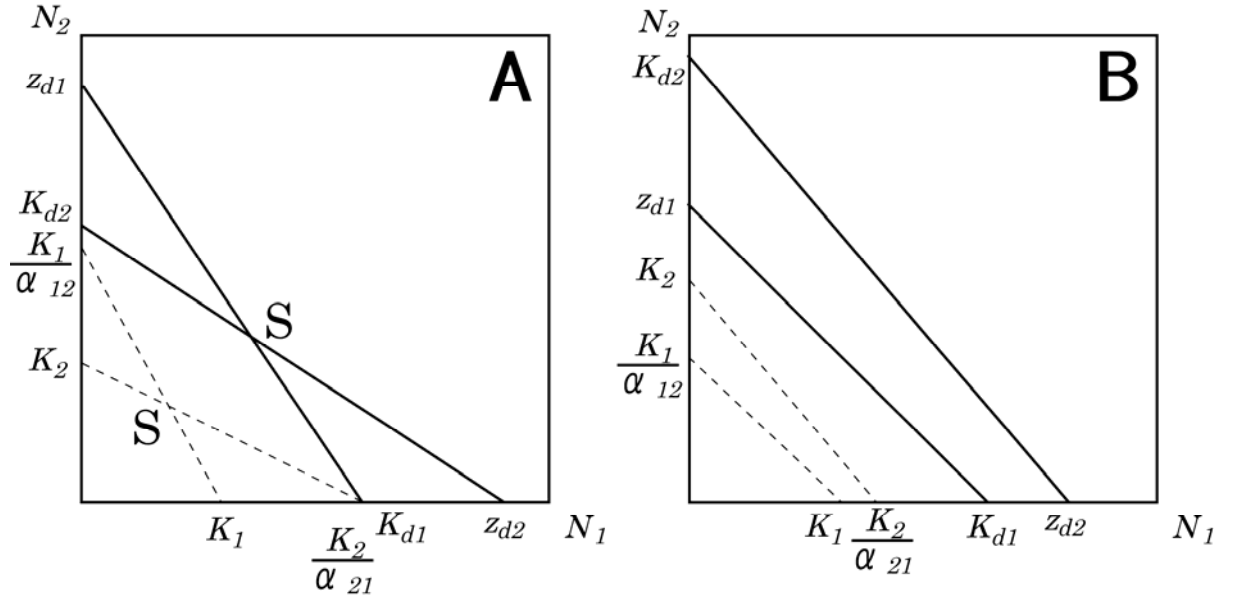
Fig. 3 - Phase planes for positive density-dependence with the Lotka-Volterra competition (Equations 1,3-5). The zero-growth isoclines are a straight line parallel to that of competition only, anchored at (K_{d1}, 0) and (0, z_{d1}) for $i = 1$, or at (0, K_{d2}) and (z_{d2}, 0) for $i = 2$. (A) Coexistence is possible under competition only ($\mathbf{S}$: stable equilibrium). (B) Coexistence is impossible under competition only. The isoclines are not only parallel to, but also proportional to the original competition-only isoclines, that is $z_{di} = K_{di} / \alpha_{ij}$ ($i,j=1, 2$).
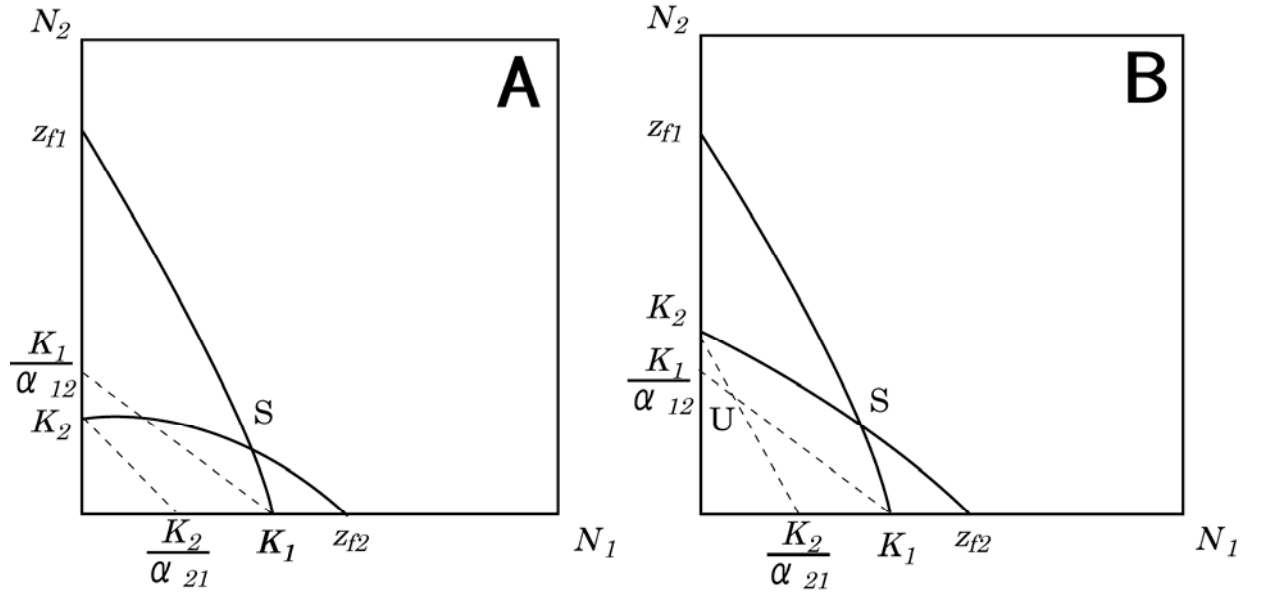
Fig. 4 - Phase planes for positive frequency-dependence with the Lotka-Volterra competition (Equations 2-5). The zero-growth isoclines are a concave curve anchored at $(K_1, 0)$ and $(0, z_{f1})$ for $i = 1$, or at $(0, K_2)$ and $(z_{f2}, 0)$ for $i = 2$. The letters **S** and **U** indicates stable and unstable coexistent equilibria, respectively. (A) Coexistence is achieved ($z_{f2} > K_1$) when species S_1 only survives under competition only. (B) Coexistence is achieved ($z_{f2} > K_1$ and $z_{f1} > K_2$) when either S_1 or S_2 survives under competition only.
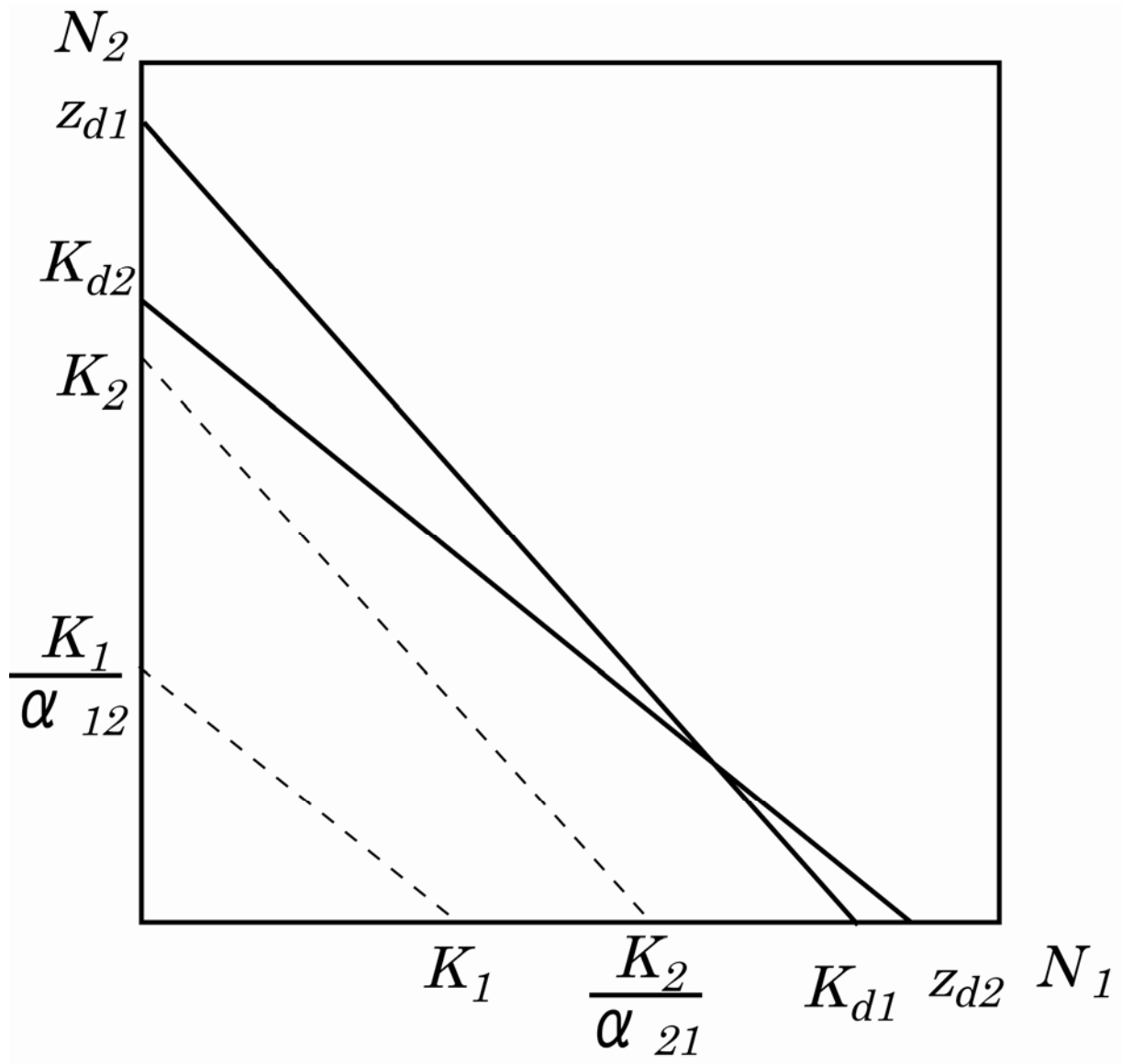
Fig. 5　Phase planes for positive density-dependence with the Lotka-Volterra

competition (Equations 1,3-5).