



# Intraspecific niche flexibility facilitates species coexistence in a competitive community with a fluctuating environment

Atsushi Yamauchi and Takeshi Miki

A. Yamauchi (*a-yama@ecology.kyoto-u.ac.jp*) and T. Miki, Center for Ecological Research, Kyoto University, Hirano 2-509-3, JP-520-2113 Otsu, Japan. AY also at: PRESTO, Japan Science and Technology Agency, Honcho 4-1-8, JP-332-0012 Kawaguchi, Japan.

We analyzed the role of niche usage flexibility (i.e. niche width) in promoting species coexistence in competitive communities in a one-dimensional niche space. We included two types of stochasticity, namely, a random sampling effect of community founding and environmental fluctuation. Fluctuation was further divided into two categories: niche-independent fluctuation (synchronized over the niche space) and niche-dependent fluctuation (variable among individual niche positions). In the analysis, two types of genetic and inheritance systems of individual niche position were considered, i.e. sexual reproduction with multiple loci and asexual reproduction with phenotypic plasticity. We found that niche usage flexibility promoted species diversity only under restricted situations when the environment was constant, but it generally promoted diversity when the environment fluctuated. In particular, under niche-independent fluctuation, niche usage flexibility significantly enhanced species diversity. In contrast, the analysis also predicted that when niche flexibility was constant, species diversity decreased with increasing environmental correlation between neighboring niches.

MacArthur and colleagues pioneered the theoretical study of the coexistence of competitive species in niche space, investigating this problem from two parallel approaches, 'limiting similarity theory' (MacArthur and Levins 1967, May and MacArthur 1972) and 'species packing theory' (MacArthur 1969, 1970). This concept has played an important role in elucidating the mechanisms of coexistence of competitive species. In particular, the limiting similarity theory provides a general basis for the coexistence of species sharing a niche.

Roughgarden (1979) analyzed the distribution of phenotypes of a single species in a niche space. In this model, each phenotype was characterized by a niche position in the space, at which each individual consumes resources within some range of the neighboring niche. In such a model, phenotypes could be regarded as species because each phenotype was assumed to reproduce clonally with exact inheritance of niche position from the parent. Roughgarden theoretically demonstrated that all phenotypes can stably and continuously coexist in the niche space under the assumption of a Gaussian fitness function, in which both the competition function and carrying capacity have Gaussian forms. Sasaki and Ellner (1995) also analyzed the evolutionarily stable distribution of phenotypes in niche space. They demonstrated that a continuous phenotypic distribution can be in an evolutionarily stable state (ESS; Maynard Smith 1982) only under restricted conditions (including a Gaussian fitness function), indicating that the coexistence of all phenotypes was not general (Sasaki 1997).

Further developing this approach, Szabó and Meszéna (2006) studied the effects of the functional form of carrying capacity on phenotypic distribution over the niche space and showed that a non-Gaussian carrying capacity generally caused a discontinuous phenotypic distribution. These studies show that the functional form of the fitness function is an important determinant of the distribution and coexistence of multiple species in niche space.

The limiting similarity theory has also been developed in studies of the role of character evolution in coexistence, i.e. niche differentiation by character displacement (Slatkin 1979, 1980, Taper and Case 1985, Doebeli 1996). This approach was introduced into multiple species communities by Case (1981). These studies found that flexible changes of niche usage by organisms play an important role in species coexistence. The niche flexibility can reflect intraspecific variation of niche usage (Lichstein et al. 2007). It should be noticed that even when the niche range of each species can be flexible, its available range must be constrained somewhat due to limited intraspecific variation on the time scale of population dynamics, which can affect coexistence processes (Aarssen 1983). Accordingly, the effects of the available niche range on species coexistence should also be examined.

Vellend (2006) recently studied the effect of intraspecific genotypic diversity on coexistence in multiple species communities in niche space. In the model, genotypic richness determined the range of niches available to species, within which the specific genotypic distribution could

change dynamically. He clearly demonstrated that increasing the genotypic richness (i.e. extending niche width) of each species enhances species diversity in competitive communities. However, his study was based on several specific assumptions: (1) the initial genotypic distribution was uniform within the niche range of each species, (2) reproduction was asexual with neither mutation nor migration (i.e. the niche position was fixed for each genotypic strain), (3) intraspecific and interspecific competition (interaction) were equally strong, and (4) the competition kernel is rectangular (competition intensity discontinuously changes with the distance between the niche positions of two individuals). The sensitivity of the results to these assumptions is not clear.

Species coexistence can also be influenced by various stochastic processes. The effects of environmental stochasticity on species coexistence have been well studied theoretically. Initially, such stochasticity was thought to reduce species diversity (May 1974, Feldman and Roughgarden 1975), although Turelli (1978) showed that stochasticity can influence the stability of a community either positively or negatively, depending on the functional form of the fluctuation. Recently, it was found that environmental stochasticity can promote species diversity through various processes (Chesson and Warner 1981, Chesson 1994, 2000, Chesson and Huntly 1997, Anderies and Beisner 2000). In addition to environmental stochasticity, species diversity can also be influenced by stochastic processes in community assembly, by which characteristics of the introduced species are chosen stochastically. Tilman (2004) investigated community structure, including stochasticities in the optimal niche position of species, the habitat, and demographic processes. He showed that stochasticity in species assembly affects the characteristics of the competitive community. Schwinck and Ackerly (2005) also showed that stochastic processes have a potentially important effect on diversity in niche space with environmental gradients. Accordingly, stochasticity should be considered when studying the assemblage of a competitive community in niche space. In particular, under environmental fluctuation, stochasticity of the niche position may influence the response of the community to a changing environment, by varying competition intensity in the community.

In summary, based on previous studies, the following factors should be incorporated into a single model to better understand the mechanisms maintaining species diversity in competitive communities: (1) the functional form of the fitness function, (2) a constraint on niche usage flexibility, and (3) stochastic processes. In the present analysis, we focused on intraspecific phenotypic variation as a source of niche flexibility, which enables a species to use some range of the niche. In reality, it is known that plant populations include some level of genetic variation and phenotypic variation such as photosynthetic light response (Mooney 1980), nutrient uptake (Shaver et al. 1979), and nitrogen status and photosynthetic capacity (Karlsson and Nordell 1988). Because these phenotypes are important determinants of the success of individual plants, the frequency and population dynamics of such intraspecific variation can modify the intensity of interspecific competition on niche space, which may affect the coexistence of multiple species.

Kobe (1999) empirically studied light gradient partitioning among tropical tree species, focusing on variation in seedling mortality and growth. He indicated that each species can potentially use a relatively wide range of niches, although they coexist by reducing their specific niche range to avoid niche overlap. This suggests that intraspecific variation in niche usage plays an important role in the coexistence of species through niche partitioning. However, intraspecific variation may be restricted by low genetic variation or a physiological constraint. Indeed, Kobe (1999) showed that a species can achieve high performance only within a narrow range of light conditions, which is a physiological constraint. These observations indicate that we must investigate the effects of phenotypic variation and its restriction on biodiversity to understand species coexistence in a niche space.

## Mathematical model

### Phenotypic variation, community construction and life history

In the present model, we assumed annual species that reproduce once, at the end of the season. We consider a species pool including many types of species, in which species  $i$  is characterized by its mean niche position,  $x_i$ , which is an integer value between 0 and 100. Different species can take the same mean niche position owing to the same  $x_i$  value. All species have an identical niche width,  $w$ , which is a positive odd integer value, such that species  $i$  can inhabit a niche range between  $x_i - (w-1)/2$  and  $x_i + (w-1)/2$ . The density of species  $i$  in niche  $j$  is denoted by  $n(i, j)$ , where  $x_i - (w-1)/2 \leq j \leq x_i + (w-1)/2$ . We considered a community that is constructed by randomly sampling  $N$  species from the species pool. Initially, all sampled species inhabit on their own niche position  $x_i$  with a density 1, i.e.  $n(i, x_i) = 1$ .

We separated the life history of organisms into two stages. The inheritance phase is a process that determines the phenotypic distribution in an offspring generation. In this stage, we considered the change in phenotypic distribution (realized by either inheritance of genetic information or random assignment to offspring) only, not the change in the total population density. The second stage is the population growth phase, which includes changes in subpopulation density. The density in the subpopulation changes with death and birth processes. The total growth rate in the subpopulation is determined by both environmental conditions and competition.

We measured population density immediately after the population growth phase. Accordingly, the life history of organisms starts from the inheritance phase.

### Inheritance phase

In the model, it was necessary to consider the inheritance system of niche usage patterns. If offspring exactly inherit the niche position of a parent, then conspecific subpopulations in different niche positions are independent of each other because of the absence of both individual migration and genetic flow between subpopulations. In this case, once

subpopulations become extinct they never revive even if the other conspecific subpopulations are alive in other niche positions. Such independent extinction events among subpopulations result in gradual reduction of the substantial (effective) niche width, in which case the effects of niche width may be undervalued. Accordingly, to correctly evaluate the effects of niche width, we considered two inheritance systems that continuously maintain niche diversity within species.

In the first system, we considered an inheritance system based on sexual reproduction within each species. We represent the system by using the approximate hypergeometric phenotypic model, in which the phenotypic distribution of offspring from parents with two phenotypes follows an approximate hypergeometric distribution (Shpak and Kondrashov 1999), which formulates a change in phenotypic distribution of a quantitative trait within a population under sexual reproduction. According to the model, for a trait that is coded by  $n$  additive loci in a diploid organism, mating between parents with phenotypic values  $p_1$  and  $p_2$  results in offspring with phenotypic value  $q$ , following the probability distribution

$${}_{2n}^{app}R_{p_1, p_2}(q) = \sum_{s=0}^{p_1} {}_{p_1}^{app}R_{p_1}(s) {}_{p_2}^{app}R_{p_2}(q-s) \quad (1a)$$

where

$${}_{p_1}^{app}R_{p_1}(s) = H(p, \max[p, s + p - 2n]) \quad (1b)$$

and

$$H(u, v) = \frac{\binom{u}{v} \binom{u}{v-u}}{\binom{2u}{u}} \quad (1c)$$

In this model, phenotypic variation in offspring is produced by recombination of loci and segregation of alleles, continuously producing phenotypic variation within a specific population. Here we considered diploid organisms with six loci (a total of 12 loci) with two alleles, involving additive effects of alleles with phenotypic value  $z$ . Each allele is assumed to express a genotypic value of either 0 or 1, resulting in 13 phenotypes ( $0 \leq z \leq 12$ ). It should be remarked that the hypergeometric distribution model is limited by assumptions. The model is adequate under strong competition among similar phenotypes, but useless under strong selection that violates intra-phenotype linkage equilibrium (Shpak and Kondrashov 1999). We discuss an applicability of this model on the present analysis in the Discussion section (below).

Individual niche positions  $j$  ( $x_i - (w-1)/2 \leq j \leq x_i + (w-1)/2$ ) are determined by the phenotypic value  $z$ , for which the relationship is assumed to be

$$j = \begin{cases} x_i - \frac{w-1}{2} + \text{Floor}\left[z \frac{w}{12}\right] & \text{if } z < 12 \\ x_i + \frac{w-1}{2} & \text{if } z = 12 \end{cases} \quad (2)$$

where  $\text{Floor}\left[z \frac{w}{12}\right]$  represents a round-down function to an integer value. This relationship between phenotypic value and niche position is relatively complicated because the phenotypic values do not exactly coincide with niche positions. Since the hypergeometric model well approximates the phenotypic distribution when there are more than 10 loci (i.e. a maximum of  $z$  is greater than 10), even few niche positions ( $w \ll 10$ ) should be determined by a phenotypic range larger than 10. Accordingly, we adopted Eq. 2 as the mapping rule from phenotypic values to niche positions.

In this system, dynamic changes in the phenotypic distribution can substantially alter the niche usage pattern of each species over evolutionary time, which may make species either generalists or specialists depending on selective pressures. However, in the present model, the evolutionary change is constrained to a specific niche width. This is reasonable, because the evolution of organisms may be restricted by genetic variation in the time scale of population dynamics. From this viewpoint, the model examines the role of genetic variation in the evolution of niche usage pattern and species coexistence.

In the second system, we considered the case with no genotypic difference in niche usage between conspecific individuals. Offspring of the focal species are assumed to uniformly redistribute over their own niche range with the same density, independent of their parents. Despite of the absence of correlation between niche positions of parents and offspring, each individual well adapts to its own niche position, by which individual performance does not vary within the specific niche range. This can be justified by ‘adaptive phenotypic plasticity’ or ‘ontogenetic stochasticity’. In the ‘adaptive phenotypic plasticity’, an individual niche position is determined previous to completing ontogenesis, after which the individual develops its own phenotype to adapt to the given niche position. On the other hand, in the ‘ontogenetic stochasticity’, the individual phenotype is variably determined by the stochastic ontogeny, after which the individual chooses a niche position that corresponds to its own phenotype. Both situations can realize that a single genotype expresses various phenotypes with the adaption to each niche position. To simulate such a situation with modeling consistent with the first system, we used a similar inheritance algorithm, by which offspring are evenly distributed across phenotypes ( $0 \leq z \leq 12$ ), rather than following the hypergeometric distribution. In this reproductive system, immediately after a single reproductive event, the distribution of a species within its own specific niche range is refreshed and a fully extended, uniform distribution is achieved.

Hereafter, we refer to the first and second inheritance systems as the ‘system with sexual inheritance’ and the ‘system without inheritance,’ respectively. It should be noted that in the first system, specific niche distribution gradually changes because the allelic frequencies change from generation to generation owing to selective forces, i.e. competition and environmental conditions. It means that in the system, specific niche use evolve dynamically within a given niche width.

## Population growth phase

After the inheritance phase, the subpopulation density of species  $i$  in niche  $j$  is considered to be  $n'(i, j)$ . Subsequently, the subpopulations undergo a population growth phase, within which the density of the subpopulation changes via death and fecundity. During this phase, the density of subpopulations of species  $i$  in niche position  $j$  changes according to the following dynamics

$$n''(i, j) = \left\{ (1 + r) - \sum_k \sum_l \alpha_{i,j,k,l} n'(k, l) + \varphi_{j,t} \right\} n'(i, j) \quad (3)$$

In this equation,  $1 + r$  is the baseline growth rate of the subpopulation, while  $\varphi_{j,t}$  is an environmental fluctuation in growth rate at niche position  $j$  at time  $t$  (see the next section).

The second term in brackets of Eq. 3 represents the total competitive interaction that the focal subpopulations receive from other (both conspecific and heterospecific) subpopulations. We assume that each individual in a certain niche position can use resources within a range of neighboring niche positions, based on a resource utilization function. Such a condition has often been adopted in studies on the phenotypic distribution of a species in niche space (Roughgarden 1979, Sasaki 1997), and results in competition between subpopulations in separate niche positions. It should be noted that there are two factors that determine the niche availability of a species: 'specific niche width' (the variation of niche position within a species) and 'resource utilization' (each individual can use resources near its own niche position to some degree, resulting in competition between subpopulations).

In Eq. 3,  $\alpha_{i,j,k,l}$  is a competition coefficient between subpopulations of species  $i$  at niche position  $j$  and species  $k$  at niche position  $l$ . It can be rewritten as

$$\alpha_{i,j,k,l} = \begin{cases} \alpha_1 f(j, l) & \text{if } i = l \\ \alpha_2 f(j, l) & \text{if } i \neq l \end{cases} \quad (4)$$

where  $\alpha_1$  and  $\alpha_2$  are basic intraspecific and interspecific competition (or interaction) coefficients, respectively. If the competition intensity between subpopulations is determined by an overlap of resource utilization alone, there may be no reason for the difference between the basic coefficients of intraspecific and interspecific competition. In this way, when conspecific individuals use a more similar niche, intraspecific competition tends to be more intense than interspecific competition. However, we consider that  $\alpha_1$  and  $\alpha_2$  involve effects other than competitive interactions. The existence of conspecific individuals in the same or a nearby niche position may impact the focal individual, for example, by predation avoidance or the prevalence of a pest or infectious disease. These effects may modify the competitive interaction between conspecific individuals. Accordingly, we assume that  $\alpha_1$  and  $\alpha_2$  can vary between intraspecific and interspecific interactions.

In Eq. 4,  $f(j, l)$  is a competition kernel. Here we considered two types of competition kernels. The first type of kernel function is a rectangular competition kernel, formulated

$$f(j, l) = \begin{cases} g_1 & \text{if } |j - l| \leq d_R \\ g_2 & \text{if } |j - l| > d_R \end{cases} \quad (5)$$

where  $d_R$  represents the critical distance between two niche positions. In our simulation, we set  $d_R = 5$  and  $g_1/10 = g_2$ . We chose  $g_1$  to normalize the integration of function  $f$  over niche space ( $g_1(2d_R + 1) + g_2\{100 - (2d_R + 1)\}$ ) to 1. This normalization is adequate to compare the results to a different competition kernel.

The second type of kernel function is a Gaussian kernel. When Gaussian functions are used, it is important to check for artifacts. Previous studies have shown that when fitness is a continuously smooth Gaussian function, all phenotypes can coexist with a continuous distribution over the niche space (Roughgarden 1979, Sasaki and Ellner 1995, Sasaki 1997, Szabó and Meszéna 2006). Fitness is a composite of two functions, i.e. resource distribution and competition kernel. If both are represented by a Gaussian distribution, the fitness function also becomes Gaussian. In the present analysis, the resource is assumed to be distributed evenly within the niche space, which is an extreme form of a Gaussian distribution. Accordingly, to avoid the artifact of Gaussian fitness, we truncated the tails of a Gaussian function at  $d_G$ , formulated

$$f(j, l) = \begin{cases} \frac{g}{\sqrt{2\pi\sigma_G^2}} \exp\left[-\frac{(j-l)^2}{2\sigma_G^2}\right] & \text{if } |j-l| \leq d_G \\ 0 & \text{if } |j-l| > d_G \end{cases} \quad (6)$$

where  $\sigma_G^2$  represents the variance of the competition kernel. We also chose the coefficient  $g$  to normalize the integration of function  $f$  over niche space to 1.

The substantial functional forms of the competition kernels used in this analysis are illustrated in Fig. 1.

## Environmental fluctuation

To examine the effect of environmental fluctuation on the relationship between niche usage flexibility and species diversity, we introduced stochasticity into the population dynamics. We considered two types of fluctuation in growth rate, 'niche-independent fluctuation' and 'niche-dependent fluctuation.' The niche-independent fluctuation is a temporal environmental fluctuation that affects the

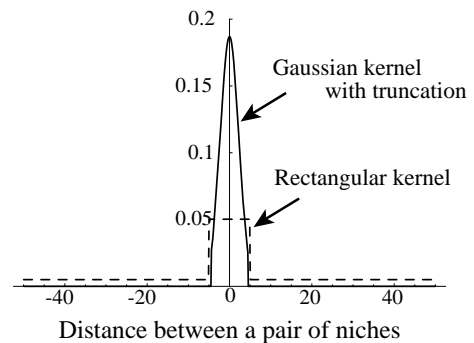


Figure 1. The substantial functional forms of competition kernels used in our model. In the rectangular kernel,  $d_R = 5$ . In the Gaussian kernel,  $\sigma_G^2 = 5$  with truncation at  $d_G = 2\sigma_G$ . Both distributions are normalized with the integration over niche spaces being 1.

conditions of all niche positions simultaneously. On the other hand, the niche-dependent fluctuation results in variation of conditions in niche positions within each year. Thus, the system includes three types of environmental variation: niche position and niche-independent and -dependent fluctuations. In this study, we considered that these factors reflect different environmental elements. For example, the niche position can be defined by resource type, while ‘niche-independent fluctuation’ results from thermal variation. On the other hand, ‘niche-dependent fluctuation’ is a variation of the growth rate, depending on individual niche position, which may reflect the annual resource supply of the niche. Because we assumed that each individual can use resources within a range of neighboring niche positions, the growth rate of the focal subpopulation may be affected by the conditions of neighboring niches within that range, which implies a correlation between the growth rates of subpopulations and neighboring niches. In addition to this, similar niche types may have similar conditions in fluctuation. Accordingly, we include such those effect by considering the autocorrelation of niche-dependent fluctuation within neighboring niches (below).

According to the two types of environmental fluctuation, the environmental fluctuation term in Eq. 3 can be formulated as

$$\phi_{j,t} = \omega_t + \delta_{j,t} \quad (7)$$

The variable  $\omega_t$  changes with time  $t$ , the effect of which is shared by all niche positions  $j$ , while  $\delta_{j,t}$  varies with both niche position and time. We considered the niche-independent fluctuation  $\omega_t$  to be a Gaussian random variable (white noise) with a mean 0 and a variance  $\sigma_\omega^2$ . On the other hand, the niche-dependent fluctuation  $\delta_{j,t}$  may correlate between neighboring niches, therefore,  $\delta_{j,t}$  was assumed to be a random variable with a correlation between neighboring niche types (red noise along the niche space) with a mean 0 and a variance  $\sigma_\delta^2$ . Based on Xu and Li (2003), the red noise along the niche space is produced by the following equation

$$\delta_{j,t} = c\delta_{j-1,t} + \varepsilon_{j,t} \quad (8)$$

where  $c$  is a constant determining the extent of correlation between neighboring niche types, and  $\varepsilon$  is a Gaussian random variable with a mean 0 and a variance  $\sigma_\varepsilon^2$ . Conditions between neighboring niches correlate positively and negatively when  $c > 0$  and  $c < 0$ , respectively. Controlling the value of  $c$ , we can obtain adequate ‘colored’ noises; red noise with  $c > 0$ , white noise with  $c = 0$ , and blue noise with  $c < 0$ . From Eq. 8,  $\sigma_\delta^2$  is  $\sigma_\varepsilon^2/(1 - c^2)$ . Accordingly, the mean and variance of total fluctuation  $\phi_{j,t}$  can be represented by

$$\bar{\phi} = 0 \quad (9a)$$

$$\sigma_\phi^2 = \sigma_\omega^2 + \frac{\sigma_\varepsilon^2}{1 - c^2} \quad (9b)$$

respectively. It should be noted that Eq. 9b is valid for an infinitely long niche space and for  $|c| < 1$ .

In numerical calculations, values of  $\delta_{j,t}$  are determined recursively from  $\delta_{0,t}$  to  $\delta_{100,t}$  following Eq. 8, where those values are possibly influenced by the initial value  $\delta_{0,t}$ . To avoid an influence of the initial value in the numerical

calculation, we virtually considered the niche range  $-20 \leq j < 0$ . We randomly chose  $\delta_{-20,t}$  by following a Gaussian probability distribution with a mean 0 and a variance  $\sigma_\varepsilon^2$  and calculated  $\delta_{j,t}$  ( $-20 < j \leq 0$ ) by Eq. 8. After this procedure, the effect of the initial value  $\delta_{-20,t}$  can approximately disappear at  $\delta_{0,t}$ . Subsequently, we determined  $\delta_{j,t}$  from  $j = 0$  to 100. Definitions of parameters and variables used in the present model are summarized in Table 1.

## Results

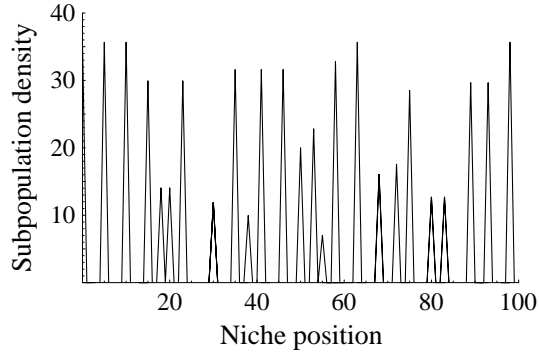
We investigated the effects of niche flexibility within species on species diversity, focusing on some factors also considered by Vellend (2006), although with different terminology. It should be noted that ‘niche breadth’ and ‘potential genotypic range’ in Vellend’s study correspond with ‘competition kernel’ and ‘specific niche width (niche flexibility)’ in our study, respectively.

Based on the above formulations, we examined the effects of niche width on species diversity using computer simulations. In a single simulation, community dynamics were pursued for 1000 time steps. Preliminary simulations indicated that this period is possibly sufficient for a community to reach a quasi equilibrium state in species number even with stochasticity. If the density of a subpopulation became negative during the calculation, it was replaced by 0. At the final time step, we determined the

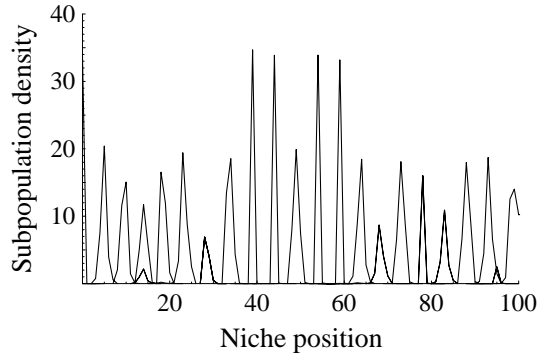
Table 1. Definitions of parameters and variables.

Character	Description
(General)	
$x_i$	Mean niche position of species $i$
$w$	Niche width of species
$n(i,j)$	Density of species $i$ in niche position $j$
$r$	Population growth rate
$\alpha_{i,j,k,l}$	Competition coefficient between subpopulations of species $i$ at niche position $j$ and species $k$ at niche position $l$
$\alpha_1, \alpha_2$	Basic intraspecific and interspecific competition coefficients
$f(j,l)$	Competition kernel between niche positions $j$ and $l$
$\phi_{j,t}$	Environmental fluctuation at niche position $j$ at time $t$
$\sigma_\phi^2$	Variance in $\phi_{j,t}$
$\omega_t$	Niche-independent environmental fluctuation at time $t$
$\sigma_\omega^2$	Variance in $\omega_t$
$\delta_{j,t}$	Niche-dependent environmental fluctuation at niche position $j$ at time $t$
$\sigma_\delta^2$	Variance in $\delta_{j,t}$
$c$	Correlation between environmental conditions of neighboring niche types
$\varepsilon_{j,t}$	Niche-dependent environmental fluctuation without correlation at niche position $j$ at time $t$
$\sigma_\varepsilon^2$	Variance in $\varepsilon_{j,t}$
(Specific for rectangular competition kernel)	
$d_R$	Critical distance between two niche positions
$g_1, g_2$	Competition intensities
(Specific for Gaussian competition kernel)	
$\sigma_G^2$	Variance in competition kernel
$d_G$	Critical distance between two niche positions (truncation)
$g$	Basal competition intensity

(a) niche width = 1, 30 of 50 species remain



(b) niche width = 5, 42 of 50 species remain



(c) niche width = 9, 47 of 50 species remain

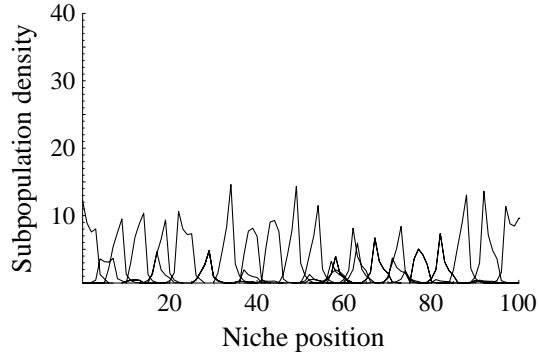


Figure 2. Examples of species distribution after 1000 time steps, where 50 species are initially introduced into the niche space. Niche width is 1, 5 and 9 in (a), (b) and (c), respectively. Sexual reproduction is assumed with a constant environment and a Gaussian competition kernel with truncation at  $d_G = 2\sigma_G$ . The baseline growth rate  $1+r$  is set at 2 ( $r=1$ ), and  $\alpha_1=0.15$  and  $\alpha_2=0.15$ . (These conditions are the same as in Fig. 3b[ii]).

number of remaining species with a total density greater than  $10^{-6}$ . Examples of final species distributions are illustrated in Fig. 2, which suggests that species diversity possibly increases with niche width in some situations.

### Constant environment

Initially, we assumed that the growth rate of a subpopulation is constant both spatially and temporally, where  $\phi_{i,t}$  is

zero. The results are illustrated in Fig. 3 and 4 for systems without and with sexual inheritance, respectively. As shown in Fig. 3a, in the system without inheritance with a rectangular competition kernel, species diversity increases with increasing niche width when the intensity of intraspecific competition is greater than or equal to that of interspecific competition ( $\alpha_1 \geq \alpha_2$ ). Figure 3b shows that in the system without inheritance with the Gaussian kernel truncated at  $2\sigma_G$ , a weaker but similar tendency is also observed when intraspecific and interspecific competition are equally strong ( $\alpha_1 = \alpha_2$ ). However, Fig. 3c shows that when the Gaussian kernel is truncated at  $3\sigma_G$ , increasing niche width does not promote diversity.

According to Fig. 4, the system with sexual inheritance has almost identical results to the system without inheritance. A single difference can be detected between Fig. 3a(ii) and 4a(ii). With a rectangular kernel, when intra- and interspecific competition are equal ( $\alpha_1 = \alpha_2$ ), species diversity increases with increasing niche width without inheritance (Fig. 3a[ii]), but not with sexual inheritance (Fig. 4a[ii]). In the absence of inheritance, the phenotypic distribution is assumed to be uniform in a single reproductive phase, while in the presence of sexual inheritance, the diffusion in niche space is realized relatively slowly through the segregation of alleles and recombination. In the sexual case, species cannot effectively use a wider range of niches, making the system with sexual inheritance unlikely to enjoy the advantage of a wider niche range. On the other hand, with a Gaussian kernel, species diversity increases with increasing niche width even with sexual inheritance (Fig. 4b[ii]). This indicates that a relatively smooth kernel (even with truncation) can suppress the disadvantage of a low diffusion rate on niche space.

Importantly, Fig. 3 and 4 indicate that with a Gaussian competition kernel, positive relationships between species diversity and niche width are observed only when the strength of intraspecific and interspecific competition is equal ( $\alpha_1 = \alpha_2$ ). With a rectangular kernel, this relationship also occurs when intraspecific competition is stronger than interspecific competition ( $\alpha_1 > \alpha_2$ ), although it may result from the extremely discontinuous form of that kernel function. In addition, when the Gaussian kernel function has a longer tail (truncated at a more distant position from the mean), the positive relationship tends to be weak. Accordingly, we can conclude that extended niche usage can promote species diversity under restricted situations.

In either the rectangular or Gaussian competition kernel, the extent of diversity significantly varies depending on the relationship between intraspecific and interspecific competition strength. If intraspecific competition is more intense than interspecific competition, many species that are introduced into the habitat can coexist. Otherwise, only a few species remain. This result is consistent with well-known conditions for species coexistence, which have been studied in detail for two-species systems. Generally, lower intraspecific competition (higher interspecific competition) suppresses species coexistence because it results in positive feedback on population growth, which is inherently unstable when there are small differences in abundance (Chesson 2000).

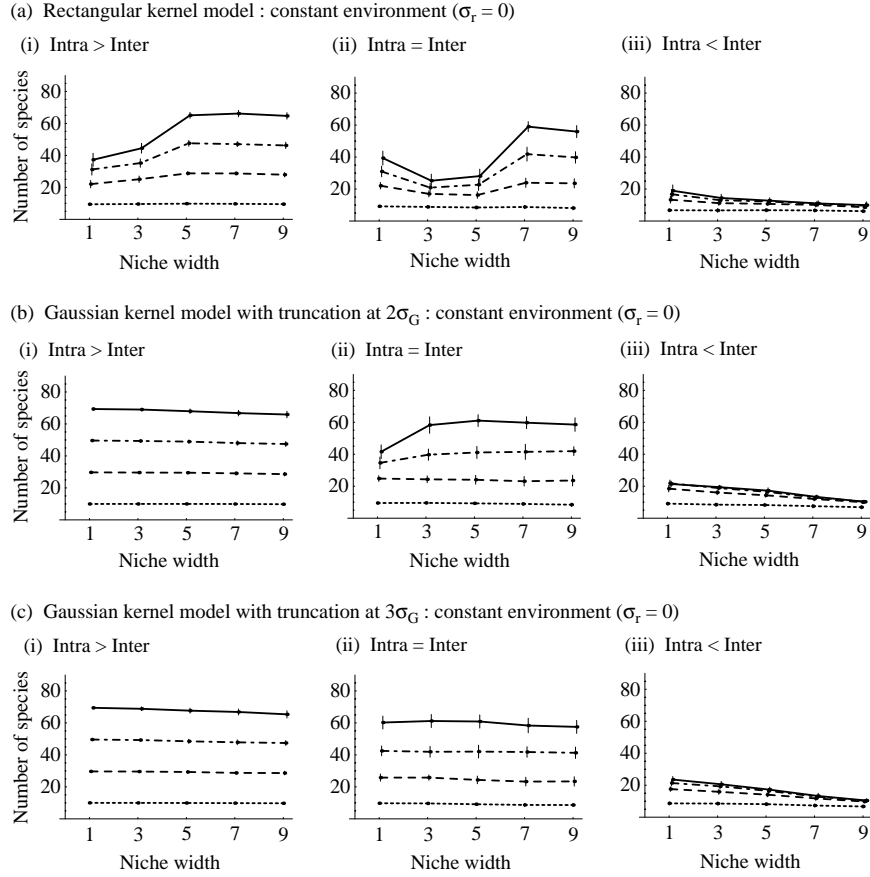


Figure 3. Relationships between niche width and species diversity without inheritance under a constant environment. Mean values of 50 trials are plotted with standard deviations shown as vertical bars. Competitive interaction is represented by (a) a rectangular competition kernel, (b) a Gaussian competition kernel with truncation at  $d_G = 2\sigma_G$ , and (c) a Gaussian competition kernel with truncation at  $d_G = 3\sigma_G$ . In either case, (i)  $\alpha_1 = 0.15$  and  $\alpha_2 = 0.1$ , (ii)  $\alpha_1 = 0.15$  and  $\alpha_2 = 0.15$ , and (iii)  $\alpha_1 = 0.1$  and  $\alpha_2 = 0.15$ . The four lines in each panel correspond to the different initial species number, as follows: 70 (solid), 50 (dash-dotted), 30 (broken), and 10 (dotted) species. The baseline growth rate  $1 + r$  is set at 2 ( $r = 1$ ).

## Variable environment

Next, we examined the effect of niche width on species diversity under a varying environment with stochasticity in the growth rate of a subpopulation  $\phi_{j,v}$ , which is characterized by mean 0 and variance  $\sigma_\phi^2$ . In the following analysis, we mainly focused on a Gaussian competition kernel with a truncation at  $2\sigma_G$ , under which niche width does not strongly affect species diversity under a constant environment (above). In the numerical calculations, we considered various types of environmental fluctuation, although those were normalized by setting the overall variance to constant values,  $\sigma_\phi^2 = 0.08$ . Accordingly, the role of niche width is comparable between different conditions of environmental fluctuation. We conducted simulations of systems both without inheritance and with sexual inheritance, although the results are qualitatively similar. Accordingly, we only illustrate those of the system with sexual inheritance.

First, we analyzed the community dynamics with niche-independent environmental fluctuation alone ( $\sigma_\omega^2 \neq 0$ ,  $\sigma_\epsilon^2 = 0$ ), the results of which are illustrated in Fig. 5. The figures indicate that niche-independent fluctuation is likely to reduce the number of coexisting species. Notably, the reduction occurs evenly over the niche width with a

rectangle competition kernel (Fig. 5a), although it tends to be more notable at smaller niche width with a Gaussian kernel, resulting in a positive correlation with niche width (Fig. 5b).

Next, we examined the dynamics with niche-dependent environment fluctuation only ( $\sigma_\epsilon^2 = 0$ ,  $\sigma_\omega^2 \neq 0$ ), with and without a correlation between neighboring niches,  $c = 0$  (white noise) and  $c > 0$  (red noise), respectively. Figure 6a illustrates the results for  $c = 0$ , while Fig. 6b shows the results for  $c > 0$ . According to these figures, when niche-dependent fluctuation is a white noise without a neighbor correlation ( $c = 0$ ), species number is extremely low only when niche positions are fixed (i.e. niche width is 1). On the other hand, if the fluctuation is a red noise with a neighbor correlation ( $c > 0$ ), a reduction in diversity is likely to occur also under a larger niche width (i.e. niche width  $> 1$ ). In Fig. 6c, we examined the joint effect of niche-independent and niche-dependent fluctuations. The figures indicate that species diversity increases with increasing niche width, the tendency of which is seen within the extended range of niche width compared to the previous cases. Consequently, extended niche usage can notably increase the number of coexisting species in an environment involving two types of fluctuations. Figure 6 was based on

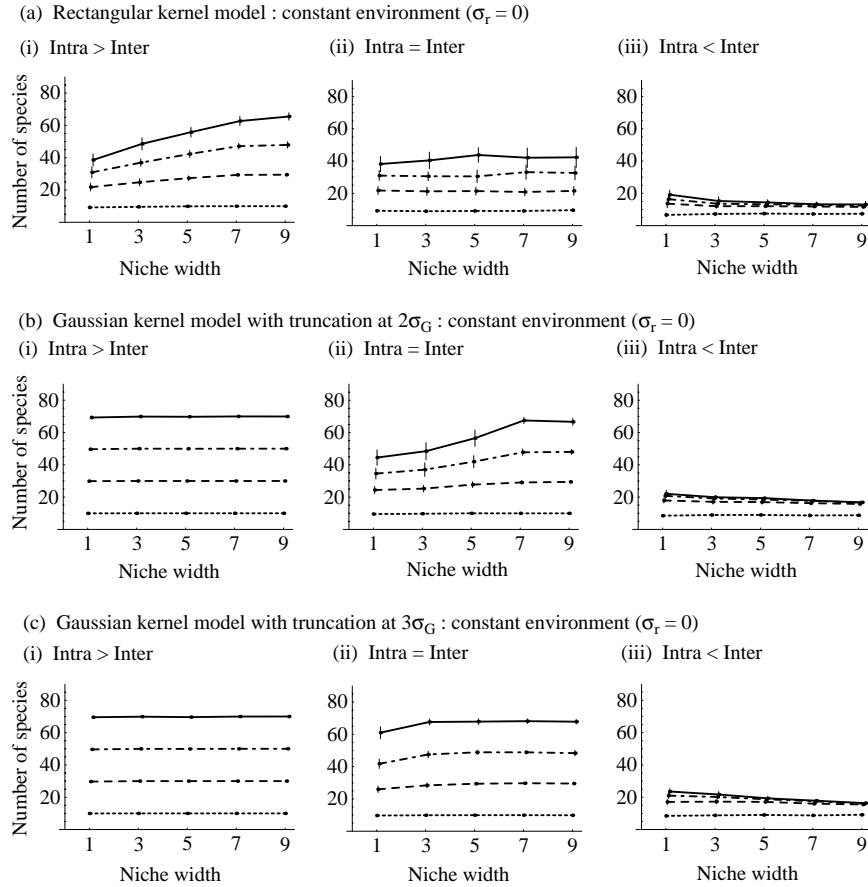


Figure 4. Relationships between niche width and species diversity with sexual inheritance under a constant environment. Conditions and parameters are as in Fig. 3.

the Gaussian competition kernel, although the tendencies are almost same with the rectangle competition kernel.

It should be noted that when stochastic processes are introduced into the population dynamics model, the population must ultimately become extinct, due to rare but significant disturbances that severely decrease population growth. Accordingly, Fig. 5 may represent only snapshots during the processes to extinction. The large variances in Fig. 5a possibly suggest that in those cases, populations become extinct even with a wide niche width. However, the small variances in Fig. 5b–d may indicate that the probability of extinction is sufficiently small such that it can be neglected at wider niche widths under those situations.

## Discussions

### Implication of the present model compared to previous studies

Recently, Vellend (2006) analyzed the relationship between genetic richness in niche usage and species diversity in competitive communities, demonstrating that species richness increases with increasing genotypic richness (i.e. extended niche width) of each species. In his model, each genotypic strain corresponds to an individual species because of the absence of genetic interactions between

them. In addition, there is no difference between intraspecific and interspecific competition. Thus, his result was a partial extension of models by Sasaki and Ellner (1995) and Sasaki (1997), i.e. a clumped phenotypic distribution in niche space. From this viewpoint, Vellend's results can be understood as follows: genotypic variation ensures that even when some phenotypes go extinct in the valleys of the phenotypic distribution, other phenotypes located outside of the valleys remain, resulting in persistence of the species.

On the other hand, our analysis shows that under a constant environment, extended niche flexibility (species niche width) can promote species diversity only with restricted conditions, i.e. a rectangular competition kernel or equal intraspecific and interspecific competition. According to the limiting similarity theory, we intuitively expect intraspecific niche variation to promote species diversity by relaxing interspecific competition, although our analysis showed only a restricted positive correlation between niche flexibility and diversity under the constant environment. In a system with two or three species, the niche differentiation possibly facilitates coexistence by niche differentiation, although it may not be true in multiple-species communities. However, once environmental fluctuations are introduced, extended niche usage effectively enhances species coexistence, owing to both modification of competition and the bet-hedging effect (below). This reveals a general role of niche width in promoting species diversity.



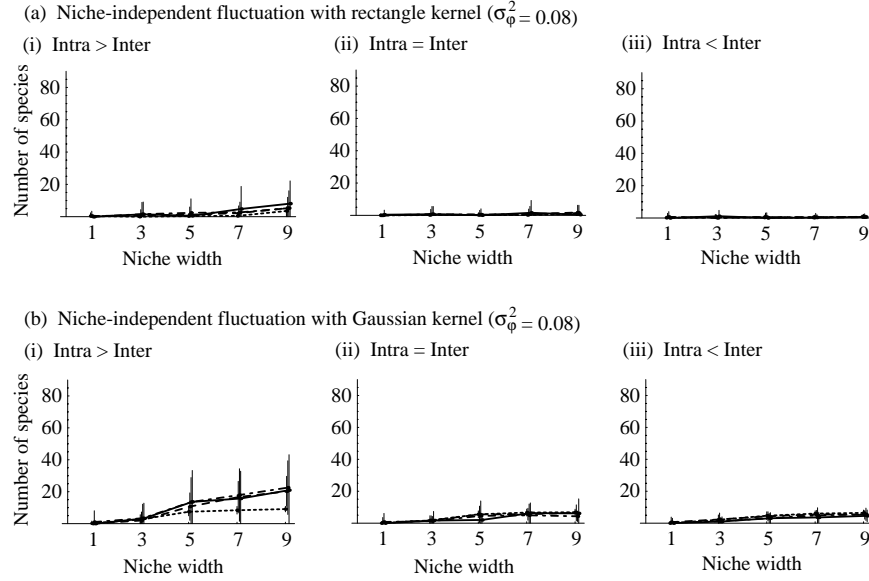


Figure 5. Relationships between niche width and species diversity with sexual inheritance under a niche-independent environment fluctuation ( $\sigma_\phi^2 = \sigma_\omega^2 = 0.08$ ) with rectangle and Gaussian competition kernels in (a) and (b), respectively. Other conditions and parameters are as in Fig. 3.

Why is niche flexibility unlikely to promote species diversity under a constant environment? It may be because niche flexibility can potentially facilitate diversity by rearran-

ging niche positions, which relaxes interspecific competition by separating two species. However, a rearranged niche position and an extended niche distribution may also

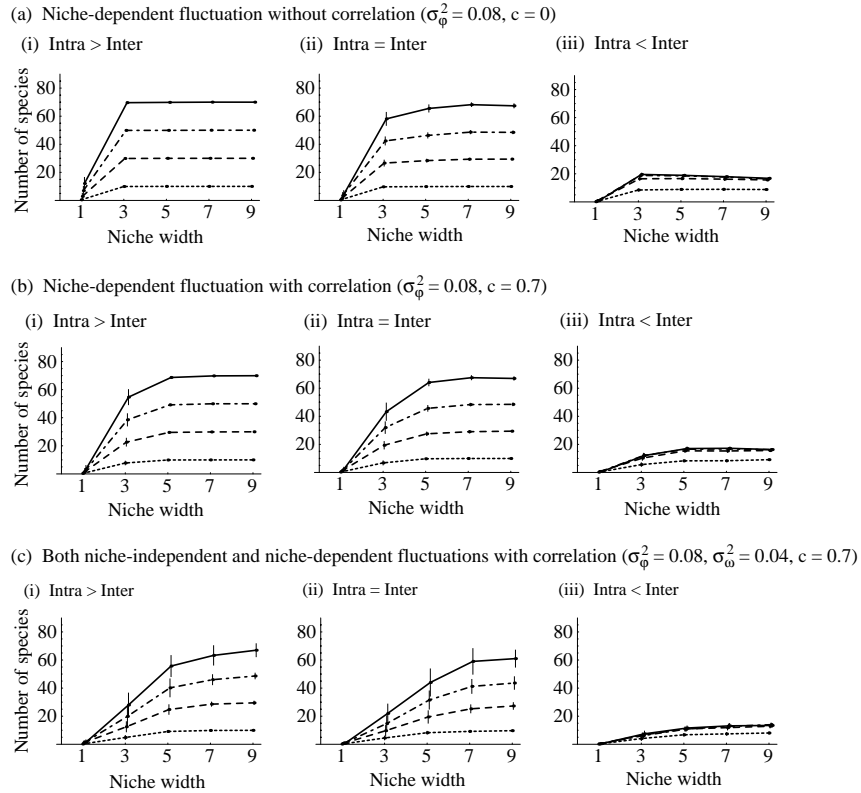


Figure 6. Relationships between niche width and species diversity with sexual inheritance under a niche-dependent environment fluctuation with Gaussian competition kernel. Fluctuation patterns are (a) niche-dependent fluctuation only, without neighbor correlation ( $\sigma_\phi^2 = 0.08$ ,  $\sigma_\omega^2 = 0$ ,  $c = 0$ ), (b) niche-dependent fluctuation only, with neighbor correlation ( $\sigma_\phi^2 = 0.08$ ,  $\sigma_\omega^2 = 0$ ,  $c = 0.7$ ), and (c) both niche-independent and dependent fluctuations with neighbor correlation ( $\sigma_\phi^2 = 0.08$ ,  $\sigma_\omega^2 = 0.04$ ,  $c = 0.7$ ). Other conditions and parameters are as in Fig. 3.

enhance interspecific competition by gathering two species. Our results show that extended niche flexibility tends to reduce species diversity when interspecific competition is more intense than intraspecific competition (Fig. 3a[iii], 3b[iii], 3c[iii], 4a[iii], 4b[iii] and 4c[iii]), which suggests a domination of negative effect of niche flexibility on diversity, i.e. the enhancement of interspecific competition. Accordingly, in multiple-species communities on niche space, the advantage of niche shift is cancelled by its disadvantage, by which species diversity is unlikely to be facilitated.

Here we assumed communities where the same competitive coefficients are shared by all species. This may be an unrealistic assumption because there are many types of species with various competitive coefficients. Accordingly, we also examined community dynamics including two types of species with higher intra- and interspecific competition. Although we did not report the consequences of such cases in the present paper, the results were intermediate between those with either high intraspecific competition or high interspecific competition. This implies that our results are robust in general situations.

### Mechanisms by which niche flexibility promotes diversity under fluctuating environment

According to the present results, different mechanisms of niche width promote species coexistence under niche-independent and -dependent fluctuating environments, respectively. Figure 5 indicated that an extended niche width can promote diversity under niche-independent fluctuation with Gaussian competition kernel (Fig. 5b), but it is unlikely with rectangle kernel (Fig. 5a). When specific niche is flexible, species can expand its own distribution within the range of niche. With the Gaussian competition kernel, it results in a decreasing intensity of intraspecific competition because the Gaussian kernel is a decreasing function of distance between niche positions on niche space. The reduction of intraspecific competition possibly moderates a sensitivity of population dynamics against environmental fluctuation, facilitating species diversity. On the contrary to this, with the rectangle competition kernel, the intensity of intraspecific competition is relatively constant against the niche distance, which does not cause the positive effect of niche width on the diversity.

On the other hand, under niche-dependent fluctuation, the promotion of coexistence can be understood as the bet-hedging effect of extended niche usage. When environmental conditions heterogeneously fluctuate over niches, the utilization of various niches is advantageous to avoid serious damage in a certain niche. However, if environmental conditions correlate between neighboring niches, bet-hedging is effective only when the niche width is larger (compare Fig. 6a with 6b).

### Diversity and pattern of environmental fluctuations

An increasing niche width suppresses reductions in diversity caused by environmental fluctuations, sustaining a high level of species diversity. The results of our analysis may provide an explanation for regional differences in species diversity. The effect of environmental fluctuations on

coexistence has been well studied (May 1974, Feldman and Roughgarden 1975, Turelli 1978, Chesson 1994, 2000, Chesson and Huntly 1997), although our analysis shows the importance of the fluctuation pattern. When species have some flexibility in niche utilization, the properties of environmental fluctuation can affect species diversity. Our results predict that for constant niche flexibility, species diversity increases in the following order: (i) a constant environment, (ii) a niche-dependent environmental fluctuation without a neighbor correlation, (iii) a niche-dependent environmental fluctuation with a neighbor correlation, (iv) both niche-dependent and niche-independent environmental fluctuations with a neighbor correlation, and (v) a niche-independent environmental fluctuation (Fig. 5, 6). This indicates that species diversity can be determined by a combination of the intensity and pattern of environmental fluctuation, and niche usage flexibility within a species.

The different impact of the two types of fluctuation on species diversity can be partly understood considering two types of average growth rate: the arithmetic mean for spatial fitness variation and a geometric mean for temporal variation (Levins 1968). When the two types of variation are of equal magnitude, the geometric mean will likely be smaller than the arithmetic mean, resulting in a notable loss of diversity under niche-independent fluctuation. In addition, the effect of niche-dependent fluctuation is influenced by the correlations among environmental conditions between neighboring niches, which is likely to reduce diversity. Consequently, to understand species diversity in a competitive community, variation and the correlations among environmental conditions must be evaluated (Chesson 2000).

### Other effects of environmental fluctuation

Niche-dependent environmental fluctuation has a restricted but remarkable effect on species diversity. Comparing the middle panel of Fig. 4b(ii) to that of Fig. 6a(ii), at niche width 3 and initial species number 70, the latter indicates higher species diversity than the former, which implies that environmental fluctuation enhances species diversity in systems with sexual inheritance. Accordingly, with sexual inheritance, niche-dependent fluctuation possibly promotes species diversity at an intermediate niche width and a high species number. Because a similar result was obtained in repeat analyses using the same parameters, this is not an extreme example. This tendency may be trivial because it is not observed with other parameter sets or in systems without inheritance, although it includes an important implication. Niche-dependent fluctuation can result in extinctions of subpopulations (but not the whole population). Especially with sexual inheritance, the recovery of a subpopulation takes time, which may reduce interspecific competition, resulting in a higher level of diversity. However, this effect may be difficult to observe because the bet-hedging effect is relatively strong at wider niche widths, in which a positive effect of niche-dependent fluctuation may be diminished.

In the present model, species diversity tends to be maximized under a constant environment and reduced by

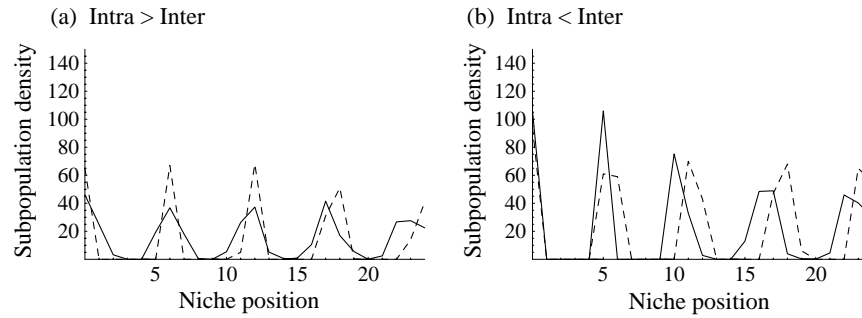


Figure 7. Comparison of species distributions between the hypergeometric distribution model (solid lines) and the individual based model (IBM; broken lines) of diploid organisms with six loci. The recombination rates between any pair of loci are set at 0.5. The niche space is bounded from 0 to 24, assuming a Gaussian competition kernel with truncation at  $d_G = 2\sigma_G$  and no environmental fluctuation. Five species with niche width 5 are introduced onto initial niche positions 2, 7, 12, 17 and 22 with 10 individuals. The baseline growth rate  $1+r$  is set at 3 ( $r=2$ ).

environmental fluctuations that affect growth rate. This is probably because the model does not involve a fluctuation-dependent coexistence mechanism, i.e. relative nonlinearity of competition and the storage effect, as pointed out by Chesson (1994, 2000). On the other hand, Chesson and Huntly (1997) reported that spatial variation can promote species diversity, owing to the presence of various successional stages in the habitat. This mechanism might be analogous to niche-dependent fluctuation in the present model, although niche-dependent fluctuation does not have such a positive effect on diversity. Because all species have the same characteristics in our model (without explicit life history), the competitive dominance relationships among species are independent of the successional stage of the focal niche.

### Effects of scaling along the niche space

The present model included three types of scales along the niche space, which are (1) the competition kernel, (2) the niche width, and (3) the heredity distribution. The relative scales among these three factors may influence species diversity, although this issue was substantially analyzed in this study. In an asexual model with phenotypic plasticity, the factor (3) disappears due to the absence of an inheritance of niche position in the system (i.e. no genetics). Since we studied the species dynamics with varying niche width (from 1 to 9), the relative scaling between factors (1) and (2) was investigated in the asexual model. On the other hand, in the sexual model, the scale of factor (3) seems to depend on the number of loci that determines the niche position. Indeed, in hypergeometric distribution model, the increasing number of loci tends to reduce a changing rate of phenotypic distribution. However, at least when the number of loci is sufficiently large ( $>10$ ), the number of loci is unlikely to alter significantly dynamics of phenotypic distribution. Accordingly, the factor (3) is not matter, too.

### Justification of the approximate hypergeometric distribution model

In the present analysis, we adopted the approximate hypergeometric distribution model to represent sexual

inheritance. The model is adequate under strong competition among similar phenotypes, but useless under strong selection that violates intra-phenotype linkage equilibrium (Shpak and Kondrashov 1999). In the present study, the applicability of the model may be determined by a balance between intraspecific and interspecific competitions. In the above simulations, we set baseline intraspecific and interspecific competition to either 0.1 or 0.15. In either case, intraspecific competition was not significantly weaker than interspecific competition, and thus the hypergeometric distribution model may be applicable. In order to examine the applicability of the model, we conduct simulations with an individual based model (IBM), results of which are compared to those of the hypergeometric distribution model. Examples of consequences are illustrated in Fig. 7, in which species distributions do not differ significantly between two models. Under the hypergeometric distribution model, species distribution tends to bias to smaller phenotypic value. The tendency is notable when the intraspecific competition is less intense than interspecific competition. Despite of such small discrepancies, we consider that the hypergeometric distribution model can be justified in the present analysis.

### Inheritance system in community dynamics

We considered two types of systems, without inheritance and with sexual inheritance. According to our analysis, there is no clear difference in the effects of niche width between those systems. While the inheritance system has been ignored in previous studies, we clearly defined the relationship between inheritance mode and intraspecific variation. Thus, the present study is the first attempt to analyze species coexistence considering both sexual reproduction and inheritance of each species explicitly. This approach provides a novel basis for the study of species diversity in competitive communities.

*Acknowledgements* – We thank A. Sasaki, N. Yamamura and members of the Center for Ecological Research, Kyoto Univ., for their comments and encouragement. This research was financially supported by the Global COE Program A06 to Kyoto University.

TM was supported by JSPS Research Fellowship for Young Scientists.

## References

- Aarssen, L. 1983. Ecological combining ability and competitive combining ability in plants: toward a general evolutionary theory of coexistence in systems of competition. – *Am. Nat.* 122: 707–731.
- Anderies, J. M. and Beisner, B. E. 2000. Fluctuating environments and phytoplankton community structure: a stochastic model. – *Am. Nat.* 155: 556–569.
- Case, T. J. 1981. Niche packing and coevolution in competition communities. – *Proc. Natl Acad. Sci. USA* 78: 5021–5025.
- Chesson, P. 1994. Multispecies competition in a variable environment. – *Theor. Popul. Biol.* 45: 227–276.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. – *Annu. Rev. Ecol. Syst.* 31: 343–366.
- Chesson, P. L. and Warner, R. R. 1981. Environmental variability promotes coexistence in lottery competitive systems. – *Am. Nat.* 117: 923–943.
- Chesson, P. L. and Huntly, N. 1997. The role of harsh and fluctuating conditions in the dynamics of ecological communities. – *Am. Nat.* 150: 519–553.
- Doebeli, M. 1996. A quantitative genetic competition model for sympatric speciation. – *J. Evol. Biol.* 9: 893–909.
- Feldman, M. W. and Roughgarden, J. 1975. A population's stationary distribution and chance of extinction in a stochastic environment with remarks on the theory of species packing. – *Theor. Popul. Biol.* 7: 197–207.
- Karlsson, P. S. and Nordell, K. O. 1988. Intraspecific variation in nitrogen status and photosynthetic capacity within mountain birch populations. – *Holarct. Ecol.* 11: 293–297.
- Kobe, R. K. 1999. Light gradient partitioning among tropical tree species through differential seedling mortality and growth. – *Ecology* 80: 187–201.
- Levins, R. 1968. *Evolution in changing environments: some theoretical explorations.* – Princeton Univ. Press.
- Lichstein, J. W. et al. 2007. Intraspecific variation and species coexistence. – *Am. Nat.* 170: 807–818.
- MacArthur, R. 1969. Species packing, and what interspecies competition minimizes. – *Proc. Natl Acad. Sci. USA* 64: 1369–1371.
- MacArthur, R. 1970. Species packing and competitive equilibrium for many species. – *Theor. Popul. Biol.* 1: 1–11.
- MacArthur, R. and Levins, R. 1967. The limiting similarity, convergence, and divergence of coexisting species. – *Am. Nat.* 101: 377–385.
- May, R. 1974. *Stability and complexity in model ecosystem* (2nd ed.). – Princeton Univ. Press.
- May, R. M. and MacArthur, R. 1972. Niche overlap as a function of environmental variability. – *Proc. Natl Acad. Sci. USA* 69: 1109–1113.
- Maynard Smith, J. 1982. *Evolution and the theory of games.* – Cambridge Univ. Press.
- Mooney, H. A. 1980. Photosynthetic plasticity of populations of *Heliotropium curassavicum* L. originating from differing thermal regimes. – *Oecologia* 45: 372–376.
- Roughgarden, J. 1979. *Theory of population genetics and evolutionary ecology: an introduction.* – Macmillan Publishing Co, pp. 499–562.
- Sasaki, A. 1997. Clumped distribution by neighborhood competition. – *J. Theor. Biol.* 186: 415–430.
- Sasaki, A. and Ellner, S. 1995. The evolutionarily stable phenotype distribution in a random environment. – *Evolution* 49: 337–350.
- Schwillk, D. W. and Ackerly, D. D. 2005. Limiting similarity and functional diversity along environmental gradients. – *Ecol. Lett.* 8: 272–281.
- Shaver, G. R. et al. 1979. Ecotypic differentiation in *Aarex aquatilis* in ice-wedge polygons in the Alaskan coastal tundra. – *J. Ecol.* 67: 1025–1046.
- Shpak, M. and Kondrashov, A. S. 1999. Applicability of the hypergeometric phenotypic model to haploid and diploid populations. – *Evolution* 53: 600–604.
- Slatkin, M. 1979. Frequency- and density-dependent selection on a quantitative character. – *Genetics* 93: 755–771.
- Slatkin, M. 1980. Ecological character displacement. – *Ecology* 61: 163–177.
- Szabó, P. and Meszéna, G. 2006. Limiting similarity revisited. – *Oikos* 112: 612–619.
- Taper, M. L. and Case, T. J. 1985. Quantitative genetic models for the coevolution of character displacement. – *Ecology* 66: 355–371.
- Tilman, D. 2004. Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. – *Proc. Natl Acad. Sci. USA* 101: 10854–10861.
- Turelli, M. 1978. A reexamination of stability in randomly varying versus deterministic environments with comments on stochastic theory of limiting similarity. – *Theor. Popul. Biol.* 13: 244–267.
- Vellend, M. 2006. The consequences of genetic diversity in competitive communities. – *Ecology* 87: 304–311.
- Xu, C.-L. and Li, Z.-Z. 2003. Population dynamics and the color of environmental noise: a study on a three-species food chain system. – *Ecol. Res.* 18: 145–154.