

Emergence of a dynamic resource partitioning based on the coevolution of phenotypic plasticity in sympatric species

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Abstract

This paper investigates the coevolutionary dynamics of the phenotypic plasticity in the context of overlap avoidance behaviors of shared niches in sympatric species. Especially, we consider whether and how a differentiation of phenotypic plasticity can emerge under the assumption that there are no initial asymmetric relationships among coevolving species. We construct a minimal model where several different species participate in a partitioning of their shared niches, and evolve their behavioral plasticity to avoid an overlap of their niche use. By conducting evolutionary experiments with various conditions of the number of species and niches, we show that the two different types of asymmetric distributions of phenotypic plasticity emerge depending on the settings of the degree of congestion of the shared niches. In both cases, all species tended to obtain the similar amount of fitness regardless of such differences in their plasticity. We also show that the emerged distributions are coevolutionarily stable in general.

Keywords: Character displacement, learning, multi-species interactions, agent-based model, genetic algorithm.

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1. Introduction

Sharing limited resources efficiently is a universal problem in biological (Brown and Wilson, 1956), social and artificial systems (Degeys et al., 2007). In biological systems, partitioning access to resources according to time, space or resource properties is frequently observed both within and between species. Ecological character displacement is known as a mechanism that realizes such a partitioning among species. It is an evolution process of phenotypic differentiation of sympatric species caused by interspecific competition in resource use (Brown and Wilson, 1956; Slatkin, 1980; Dayan and Simberloff, 2005). If the use of a common but limited resource shared by multiple species brings about conflicts among species, a disruptive selection diversifies the resource use of the sympatric species, which realizes the partitioning of their shared resources, as a result. The recent report by Grant and Grant has shown that a Darwin’s finch species on an undisturbed Galapagos island diverged in beak size from a competitor species 22 years after the competitor’s arrival (Grant and Grant, 2006), and Kirschel et al. also reported the character displacement of song (frequency) as well as morphology (bill and body sizes) in African tinker birds (Kirschel et al., 2009). It was also reported that, in some cases, the relative difference in the exploited niches was much more critical than their absolute positions on the resource gradient, and thus “crossovers” in character displacement in different habitats were observed (Cody, 1973).

There have been various mathematical models of ecological character displacement (Slatkin, 1980; Doebeli, 1996; Konuma and Chiba, 2007; Goldberg et al., 2012)(Leimar et al., 2013) including MacArthur’s seminal work on “species packing” (MacArthur, 1969) and “limiting similarity” (MacArthur and Levins, 1967). For example, Slatkin et al. constructed a two-species model based on quantitative genetics with several assumptions, and showed that the key conditions for substantial displacement were either differences in resource spectra of the two species or constraints on trait variance (Slatkin, 1980). Various models with relaxed, sophisticated or realistic assumptions have been proposed, investigating the conditions for character displacement or species coexistence to occur (e.g., (Doebeli, 1996; Konuma and Chiba, 2007; Goldberg et al., 2012)(Leimar et al., 2013))

Although it has been recognized that phenotypic differences should have a genetic basis in this context (Schluter and McPhail, 1992), roles of phenotypic plasticity in character displacement or coevolution of multiple species

are discussed recently (Pfennig and Pfennig, 2010, 2012a,b). A niche width, the available range of resource use on a niche axis, can represent the phenotypic variance caused by developmental plasticity or learning. Yamauchi and Miki discussed effects of intraspecific diversity, termed niche flexibility, on the species diversity under the two different assumptions in which the distribution of niche use for each species is evolvable within the range of the maximal niche width or in which the use is evenly distributed over that niche width due to the phenotypic plasticity (Yamauchi and Miki, 2009). They showed that the larger maximum flexibility of niche use can promote species diversity under fluctuating environments in general. Ackermann and Doebeli proposed a mathematical model in which both the position and the width of resource use by consumer individuals were allowed to evolve through the ecological dynamics of both consumer and resource, in which the individual niche width can be interpreted as the phenotypic plasticity (Ackermann and Doebeli, 2004). They showed, both analytically and numerically, that whether the adaptive diversification of resource use composed of several subgroups with the smaller niche width (specialists) emerges or a single group with the larger niche width (generalists) dominates the population depends on the inherent costs or benefits of widening the niche.

In this paper, we focus on another type of the phenotypic plasticity in coevolution of multiple species: the frequency of changes in the resource use, rather than the available range of resource use on a niche axis. There can be a situation in which it is necessary for each individual to adapt in an “ad-hoc” manner because the adaptive niche can vary through social interactions among species through their lifetime. In such a dynamic resource partitioning¹, it is necessary for them to adjust its resource use depending on changing resource uses of their neighbors. The temporal space is one of the typical resource spectrums in which the sympatric species have to adapt in such an ad-hoc manner. This is because the temporal space is basically shared by neighboring species that communicate with sounds in addition to the fact if it is necessary for them to adapt to interference by unexpected background noises (Brumm and Slabbekoorn, 2005).

For example, rather than vocalize at random, birds may divide up sound

¹We use the term “dynamic resource partitioning” (or simply “resource partitioning”) in order to describe a process in which several species partition their resource use via their social and lifetime interactions rather than their genetic evolution process.

space in such a manner that they avoid overlap with the songs of other bird species in order to communicate with neighbors efficiently. There have been empirical studies on the temporal partitioning or overlap avoidance of singing behaviors of songbirds with various time scales (Cody and Brown, 1969; Ficken and Ficken, 1974; Popp et al., 1985; Brumm, 2006; Planqué and Slabbekoorn, 2008; Suzuki et al., 2012). Cody and Brown's pioneering study showed that Wrentit and Bewick's Wren tended to cycle their song activity with a half-period of about 50 minutes asynchronously (Cody and Brown, 1969). Recently, Planqué and Slabbekoorn investigated both spectral (frequency) segregation and temporal avoidance in a complex rainforest community (Peruvian bird assemblage), showing that there was significantly less temporal overlap at frequencies more often used by multiple bird species. The temporal overlap avoidance of acoustic behaviors have been observed in other various species such as frogs (Schwartz and Wells, 1984) and insects (Greenfield, 1988).

This type of resource partitioning behavior can be interpreted as an adaptive phenotypic plasticity in that an individual modifies its resource exploiting strategy actively in response to the current state of resource use by others. Recently, Pfennig and Pfennig described that any reaction norm that evolves in response to competitive mediated selection would constitute character displacement (Pfennig and Pfennig, 2012b), and that how character displacement can be mediated either by genetically canalized changes or by phenotypic plasticity, and discussed how these factors can mutually interact with each other (Pfennig and Pfennig, 2012a). Effects of adaptive plasticity on evolution has been focused on recently, including the Baldwin effect (Sznajder et al., 2012). The evolution of phenotypic plasticity (or learning) has been discussed in a social or game theoretical context (Katsnelson et al., 2012; Suzuki and Arita, 2013), a rapid adaptation of a predator-induced phenotypic plasticity in prey-predator relationships (Yamamichi et al., 2011), etc. In addition, phenotypic plasticity has also been getting much attention in the field of community ecology. It has been reported that the developmental plasticity of traits in plants (e.g., roots and leaves) can reduce intra- and inter-specific competitions for resources (e.g., chemicals and lights) (Ashton et al., 2010; Schiffers et al., 2011). However, as far as we know, there have been few theoretical or computational approaches that discussed the emergence of dynamic resource partitioning from this viewpoint of the coevolution of phenotypic plasticity in sympatric species.

In the study reported here, we focus on this type of dynamic resource

partitioning which can be realized through interactions among individuals. In our previous work, we discussed whether and how the sound space partitioning can be realized by the coevolution of the phenotypic plasticity to increase communication efficiency in bird communities (Suzuki et al., 2012). We conducted an evolutionary simulation of the temporal overlap avoidance behaviors in the sympatric species with different species specific length of songs. An interesting finding is that the species with the longest song typically evolves to become dominant – what we term the “driver species.” The driver species does not change the timing of its song to avoid overlap very much, but keeps its original periodicity, while species with shorter songs adapt to fit into the remaining time segments.

Our purpose of this paper is to obtain more general and fundamental mechanism of such a complex scenario in the coevolution of behavioral plasticity of sympatric species in the context of social interactions for efficient resource partitioning. Specifically, we consider whether and how a differentiation of phenotypic plasticity can emerge under the assumption that there are no initial asymmetric relationships among coevolving species. For this purpose, we construct a minimal model where several different species participate in a partitioning of their shared niches, and evolve their behavioral plasticity to avoid an overlap of their niche use. We conduct evolutionary experiments with various conditions of the number of species and the number of niches. We show that the two different types of asymmetric distributions of phenotypic plasticity emerge depending on the settings of the degree of congestion of the shared niches. It should be noted that, in both cases, all species tended to obtain the similar amount of fitness regardless of such differences in their plasticity. We show that the emerged distributions are coevolutionarily stable in general, and also show that such asymmetric relationship does not emerge in a genetically fixed-trait version of our model.

2. Model

We assume S different species and the population of each species is composed of N individuals. We assume N groups, each in which S individuals share niches. For each species, all individuals are randomly assigned to the N groups without duplication. In other words, each group is composed of S individuals of S different species. Figure 1 shows an example of a group composed of the three individuals of the three different species that share the four niches. The iterative interaction is conducted among the members

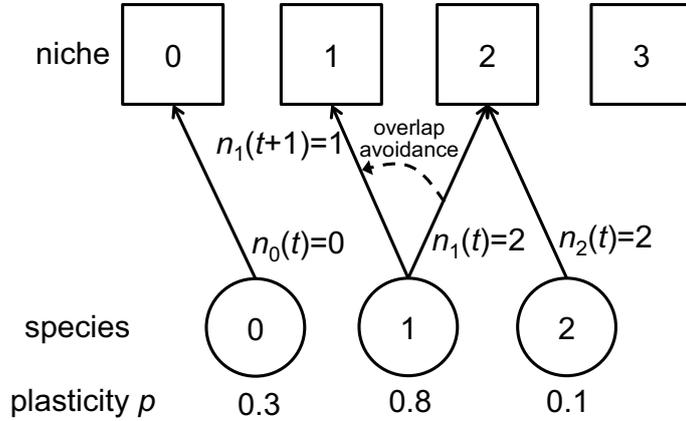


Figure 1: An example of interactions among sympatric species when $L=4$ and $S=3$. At time t , there is an overlap of the use of the niche 2 by the species 1 and 2. At time $t+1$, this overlap was resolved by the change in the niche use from 2 to 1 by the species 2 due to its high phenotypic plasticity.

of each group independently in order to determine the fitness contribution of each individual as follows:

We assume that there are L niches for each group as illustrated in Fig. 1. We can regard their niche space as one of any kind of resource types (e.g., temporal, spatial, frequency and nutrient spaces) although we do not assume a specific topological relationship among niches. Each individual s of the species S in a group chooses a niche $n_s(t)$ in order to obtain the benefit from it at time t . It obtains the fitness contribution $f_s(t)$ as follows:

$$f_s(t) = \begin{cases} 1 & \text{if } d_{n_s(t)}(t) = 1, \\ 0 & \text{otherwise,} \end{cases} \quad (1)$$

where $d_l(t)$ is the number of individuals in the group that used the l -th niche at time t . This equation means that an individual can obtain the fitness contribution only when the focal individual has dominated a niche, otherwise it obtains no fitness contribution.

Each individual s has a genetically determined probability gp_s interpreted as its behavioral plasticity. Each individual decides which niche in the next time step $t+1$ by following the equation:

$$n_s(t+1) = \begin{cases} \text{rnd_b}(L, n_s(t)) & \text{if } d_{n_s(t)}(t) \geq 2 \text{ and with the prob. } gp_s, \\ n_s(t) & \text{otherwise,} \end{cases} \quad (2)$$

where, $\text{rnd_b}(x, y)$ is a random integer value taken from 0 to $x-1$ except for y . This means that if the niche use of an individual overlaps with the use of others, the focal individual decides to change the niche to use with a genetically determined probability gp_s . If it decides to change, it uses a randomly chosen niche at time $t + 1$ except the one used by itself at time t . Otherwise, the focal individual continues to use the same niche at time $t + 1$ as the one used at time t . We adopt this trial-and-error procedure as one of the simplest implementations of reinforcement learning.

In addition, we assumed an occurrence of an external noise that randomizes the niche use of all individuals. At each time step, all individuals choose a niche randomly from L niches with a small probability p_n without performing any avoidance behaviors based on their plasticity, regardless of their niche use in the previous step.

These interactions are conducted for R time steps, and the fitness of each individual is taken to be the average of the fitness contribution over all time steps. Note that each individual chooses one niche randomly from L niches at the initial step of interactions.

The population of each species is evolved independently according to the genetic algorithm based on selection and mutations. It should be noted the phenotypic plasticity gp_s is genetically determined for each individual (and not for each species) and thus the sole target for selection, of which value is inherited to the offspring. The offspring in the next generation are selected from the current population using ‘‘roulette wheel selection’’ based on the Monte Carlo method (in which the probability that an individual will be chosen as a parent is proportional to its scaled fitness). The scaled fitness of each individual is defined as the relative value of the fitness of the focal individual from the minimal fitness in the population. For the plasticity gene gp_s of each offspring, a mutation occurs with a small probability p_m , which adds a small random value sampled from the uniform distribution over $[-DM, DM]$ to the current value. If the resultant value is out of the domain of the genetic value, we conduct a mutation process again.

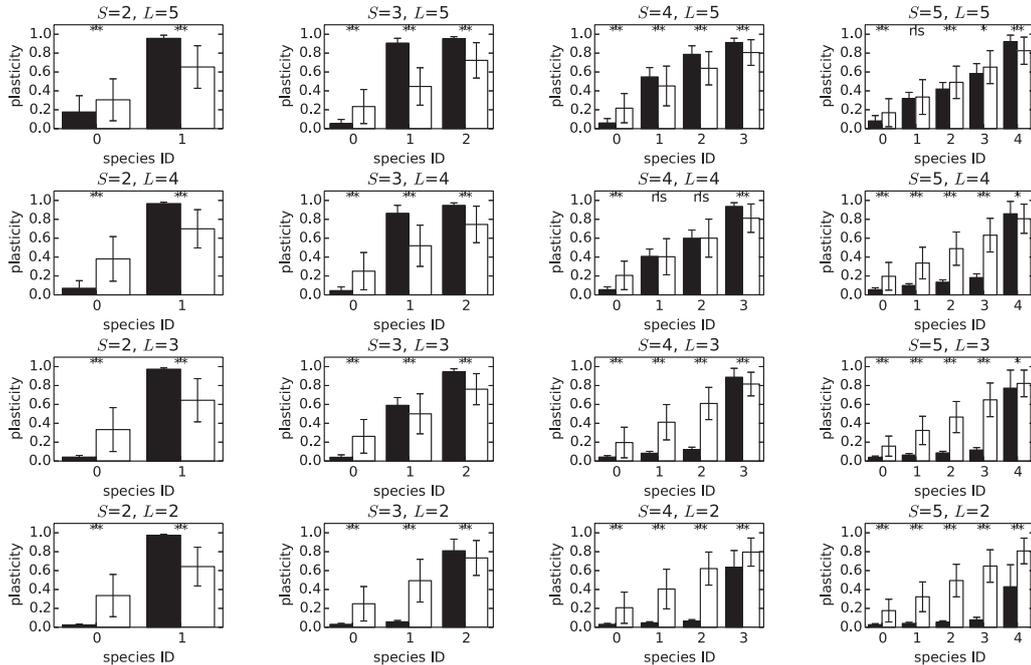


Figure 2: The average plasticity in the last generation with the different combinations of S (the number of species) and L (the number of niches). The black bars represent results with the original experiments and the white bars represent results with the control experiments. The P-values, as determined by a two-tailed t-test, are indicated by double asterisk ($P < 0.001$), asterisk ($P < 0.05$) and ns (not significant).

3. Results

We conducted experiments with various settings of S and L for 10,000 generations using $N = 200$, $R = 100$, $DM = 0.05$, $p_m = 0.01$ and $p_n = 0.03$. The initial population was generated with initial values of gp_s sampled from the uniform distribution over $[0, 1]$. All values in results are the average over 100 trials.

3.1. Control experiments

Before analyzing the coevolution of the phenotypic plasticity, we conducted control experiments in which the individuals were selected randomly regardless of the results of interactions, in order to see the effect of neutral selection on the evolution of plasticity. The white bars in Fig. 2 show the average plasticity gp_s in the last generation with the possible combinations of

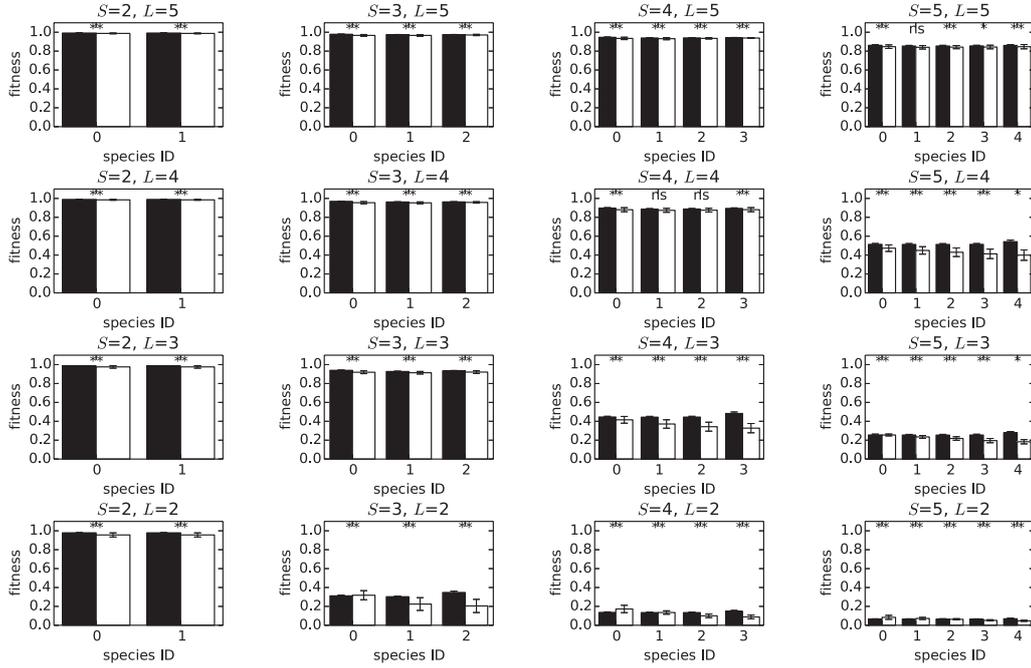


Figure 3: The average fitness in the last generation with the different combinations of S (the number of species) and L (the number of niches). Black bars: results with the original experiments. White bars: results with control experiments.

S ($=2, 3, 4$ and 5) and L ($=2, 3, 4$ and 5) in the cases of control experiments. In each subfigure, the horizontal axis corresponds to the species' ID. The ID of each species was numbered in ascending order of the average plasticity at the last generations. For example, when $S=3$, the species that has the smallest plasticity in the last generation is numbered as 0 and the one with the largest plasticity is numbered as 2.

The results show that there was a significant difference in the plasticity among species due to the genetic drifts even if there was no selection pressure in this experiment. We see that the average plasticity increased linearly as the species ID increased. This implies that the average plasticity uniformly distributed in its domain. The difference in gp_s in the original experiments from the one in the corresponding control experiments reflects the net effect of interactions among species on coevolution of the phenotypic plasticity.

The white bars in Fig. 3 also show the average fitness (but not used in the control experiments) in the same experiments as the ones in Fig. 2. When

$L \geq S$, the fitness of the all species tended to be high and there were basically no clear differences in the fitness among the all species. In these cases, there are sufficient number of niches for each species to dominate, and thus the fitness of all species are basically high because each species can find a vacant niche easily even if their plasticity evolved under the neutral evolution.

However, we see that the average fitness decreased as the plasticity of the species increased when $L < S$, in which a conflict of an occupied niche always occurs ($L < S$). It should be noted that the fitness of the most adaptive species with the largest plasticity was approximately 50% larger than the one of the least adaptive species with the smallest plasticity in the case with $S=3$ and $L=2$. The former was approximately twice as the latter in the case with $S=4$ (and 5) and $L=2$. This seems to be due to the fact that the plastic behaviors with the higher plasticity (appeared through the neutral selection) tended to be unsuccessful in such congested situations.

3.2. *The differentiation of phenotypic plasticity*

Here, we focus on the coevolution process of the phenotypic plasticity with the original experimental settings. The black bars in Fig. 2 represent the average gp_s of each species at the last generation in the original experiments. We conducted statistical tests on whether there exist statistically significant differences in the average values of the phenotypic plasticity and fitness between the original cases and the corresponding neutral cases, using a two-tailed t-test. We found that there were statistically significant differences between them in most cases (double asterisk: $P < 0.001$, asterisk: $P < 0.05$, ns: not significant)².

As a whole, we see that the evolution process of plasticity strongly depends on the combination of S and L that determines the degree of congestion of their shared niche space. It should be noted that the phenotypic plasticity tended to be significantly differentiated among species compared to the corresponding results in control experiments (white bars). In general, the plasticity of the whole species tended to be smaller when S was larger than L , and the plasticity tended to be higher when S was smaller than L .

Specifically, we can see that there are the two different types of the distribution of the evolved phenotypic plasticity among species. When (a) $L > S$

²A few exceptional cases are expected to be due to the fact that the evolved average values in the original cases were very close to those in the neutral cases by chance and there were large standard deviation in these values.

or $L = S \leq 3$, the plasticity of one species evolved to be significantly lower than the one of the corresponding species in control experiments, while the plasticity of the other species evolved to be higher. The black bars in Fig. 3 shows the average fitness of the species in the same experiments. Despite the emerged difference in the phenotypic plasticity, we see that the average fitness of all species evolved to be almost the same and slightly higher than the ones in the control experiments. This means that the emerged asymmetric relationship among species with regard to the phenotypic plasticity brought about the equal benefit to all species.

When (b) $L < S$, in which a conflict of an occupied niche always occurs, the plasticity of all species evolved to be lower than the one of the corresponding species in control experiments. This means that the lower phenotypic plasticity is adaptive in the case with the higher degree of congestion of their niche space. However, at the same time, we see that one species maintained relatively higher plasticity, while the plasticity of the other remaining species became very small. Again, it should be noted that such an asymmetric relationship made the average fitness of the all species high and equal, while there was a negative correlation between the plasticity and the fitness in the corresponding control experiments.

As a whole, we can say that adaptive and equal resource partitioning can be realized dynamically by the differentiation of the phenotypic plasticity irrespective of the degree of congestion of the niche space. However, there is a significant difference in the emerged distribution of the phenotypic plasticity between the more and less congested situations.

3.3. Dynamic resource partitioning

Next, we discuss how such an adaptive and equal resource partitioning was realized dynamically in each case by looking closer at several example interactions among species. First, we focus on the simplest case when $S = 2$ and $L = 2$ as a typical example of the case (a). Fig. 4 shows an example interaction for the initial 50 time steps among individuals in the last generation with this setting. In this case, we see that while the plasticity of the species 0 evolved to be much smaller than that in the control case, that of the species 1 evolved to be much higher than that in the control case. In this case, a niche overlap occurs with the high probability of 0.5 at the initial step because they choose one niche from the two niches randomly. In such a situation, if both individuals switch from the current niche to the other one because of their high plasticity, a collision of another resource use occurs again. This

means that the interactions among species with the high plasticity are not adaptive because their simultaneously occurring avoidance behaviors often bring further overlaps. However, if one species does not change the niche use and the other switches, both species successfully avoid exploiting the same niche without fail. Fig. 4 clearly shows that the niche overlaps due to the occurrence of a noise at the 43th step was resolved quickly by the change in the niche use of the plastic species.

Fig. 5 shows an example interaction among individuals in the last generation for the initial 50 time steps when $S=3$ and $L=3$. In this case, we also observed that one species evolved to be less plastic and the other remaining species evolved to be more plastic. Fig. 5 clearly shows that the plastic species actively avoid the overlap after the occurrences of a noise. The reason why the plasticity of the only one species became small is that if the multiple species evolved to be less plastic, a niche overlap between these two species cannot be resolved at all. Thus, it is the best collective strategy for all species that one species dominates the initial niche while the other remaining species actively change the niche to use if there is an overlap. The differences in the plasticity among the remaining species are also expected to reflect such a benefit of the differentiation of the plasticity among them due to the similar reason.

In contrast, in the case (b), the plasticity of one species tended to be high while the other species' plasticity evolved to low values. We focus on the case of $S=3$ and $L=2$ as an example of the evolved distribution in this case. Fig. 6 shows an example interaction for the initial 50 time steps among individuals in the last generation in this case. We can see that there are two typical patterns of interactions. One is the case in which the highly plastic species 2 only could obtain the fitness contribution by dominating the niche 1 while the species 0 and 2 occupied the same niche 0 for several time steps because their plasticity were very small, as observed from the "7th to 16th" and "24th to 26th" time steps. The other is one in which the plastic species 1 actively changed its niche use between 0 and 1 although it always overlapped with either species 0 or 2. In this case, the less plastic species 0 and 2 obtained the fitness contribution every two steps, while the species 0 could not obtain it at all. These patterns changed from one to the other due to the occurrence of a noise or their overlap avoidance behaviors. While the benefit that each species obtains is different between these patterns, it is expected that the evolved asymmetric distribution of the plasticity balanced the occurrences of these patterns so that all the three species obtained similar fitness. The equal

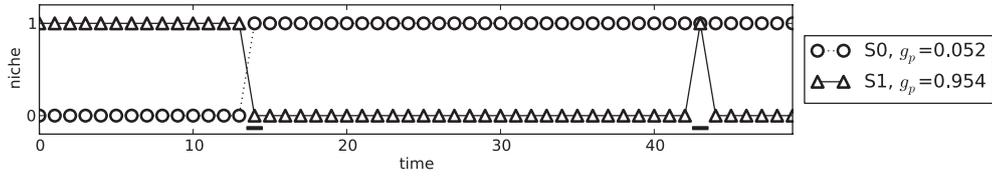


Figure 4: An example interaction among species when $S=2$ and $L=2$. The horizontal axis represents the step and the vertical axis represents the ID of the niche that each species used at the time step. The black bar on the bottom represents a noise that occurred at the corresponding step.

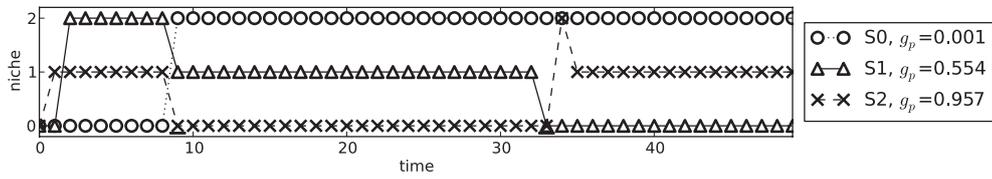


Figure 5: An example interaction among species when $S=3$ and $L=3$.

adaptivity of the fitness among the species with the different plasticity in all the cases (b) was more or less expected to be due to the similar mechanism.

3.4. Coevolutionary stability analysis

Finally, we conducted a simple analysis in order to see if the emerged distribution of the phenotypic plasticity observed in Fig. 2 is coevolutionarily stable or not. Specifically, for each set of the values of the average phenotypic plasticity at the last generation obtained in the previous experiments, shown in Fig. 2, we conducted interaction processes among individuals for R time steps under the assumption that the plasticity of an individual in one species was set to a specific value while the plasticity of the individuals of all the

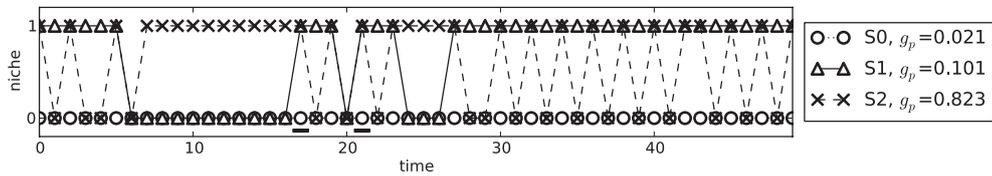


Figure 6: An example interaction among species when $S=3$ and $L=2$.

other species were fixed to the corresponding values observed in Fig. 2. We used various values of the plasticity of the focal species at the intervals of 0.02, and also used the following parameters: $R=100$ and $p_n=0.03$.

Fig. 7 shows the average fitness of the focal species with the various values of the plasticity. The x-axis represents the species ID of the focal species, and the y-axis represents the specified plasticity of the focal species. All values are the average over 1000 trials. Each star represents the corresponding value of the evolved plasticity in Fig. 2. Each open circle represents the value of the plasticity that brought about the best fitness of the focal species among the all cases of the plasticity along the y-axis. If the location of a star is sufficiently close to the corresponding open circle, we can say that there expected to be no further evolution of the plasticity of the focal species under the assumption of the fixed plasticity of the other species, because mutant individuals are less adaptive than the evolved ones. If this is true for all species, we can also say that the whole distribution of the plasticity is coevolutionarily stable in that any mutant individuals cannot invade into the population.

We see that there exists a unimodal peak on the smooth surface of the fitness values (or fitness landscape) on each y-axis, meaning that the value of the plasticity on the peak (open circle) corresponds to the expected value to which the plasticity converge if the plasticity of the focal species only evolved. Note that the reason why the fitness surface was not smooth when “ $S=5$ and $L=5$ ” and “ $S=5$ and $L=2$ ” seems to be the large effects of stochastic noises on the interactions among many individuals under the less or much congested situations. It should be noticed that each evolved plasticity (star) is significantly close to the corresponding best value (open circle). Thus, we can say that a coevolutionarily stable state emerged in all conditions in general.

3.5. Effects of experimental settings and comparisons with a genetically fixed-trait model

In order to see effects of experimental settings on the results, we conducted further experiments with different combinations of the population size N , the number of interactions R , the probability of noise p_n , the mutation probability p_m and the maximum amount of change in the plasticity due to a mutation DM . We did not observe any qualitatively different results except for minor quantitative effects of settings on the distribution of phenotypic plasticity. It should be noted that the larger degree of differentiation

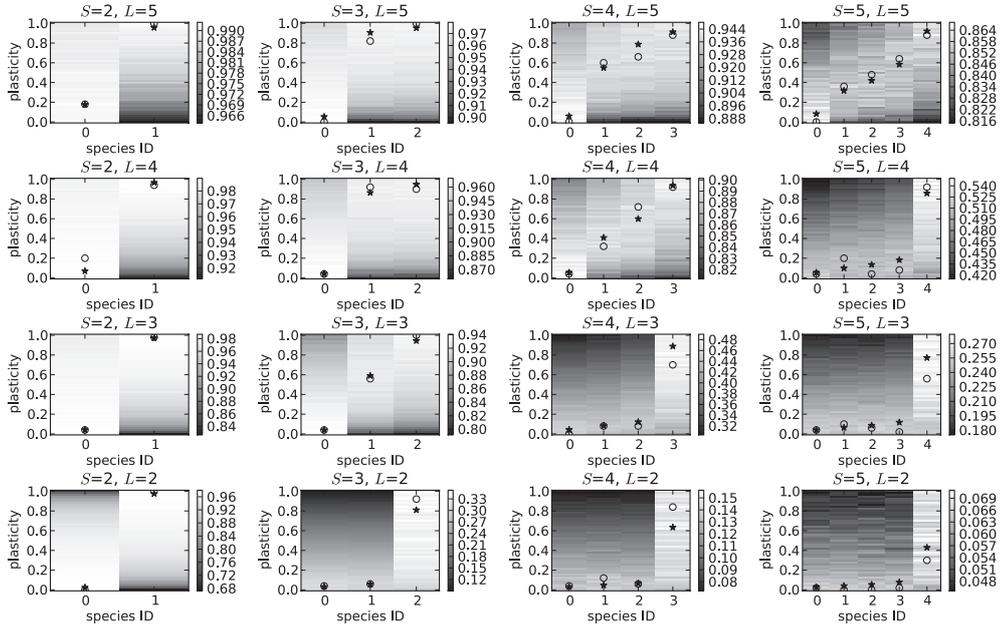


Figure 7: The fitness of the species with different settings of its plasticity under the assumption of the fixed plasticity of the other species to the corresponding ones in Fig. 2, with the different combinations of S (the number of species) and L (the number of niches).

of phenotypic plasticity between plastic and less plastic species tended to be observed when we increased p_n from 0.03 to 0.1. This is expected to be due to the increased selection pressure for the differentiation of plasticity, because the competing species were necessary to recover more frequently from disturbed niche uses caused by noise.

In the original model, we adopted an extreme case of conflict of resource use in that conflicted individuals both obtain no fitness contribution as defined in the equation (1). We conducted experiments with a relaxed condition of the fitness contribution using the equation $f_s(t) = \{d_{n_s(t)}(t)\}^{-1}$ instead of the equation (1). This assumes that the fitness contribution for an individual that have chosen a niche is inversely proportional to the number of individuals (including the focal individual itself) that have chosen that niche. It turned out that there were no significant differences in the distributions of phenotypic plasticity between the original case shown in Figure 2 and the relaxed case.

Finally, in order to see the qualitative difference between the original

case and the case with a genetically-fixed trait model, we constructed another model by slightly modifying the original model. Specifically, instead of assuming a phenotypic plasticity as a genotype to evolve, we assumed a genetically determined ID ($0, \dots, L-1$) of niche that each individual uses. We calculated the fitness of each individual by looking at the overlap of their genetically determined niche uses instead of conducting repeated interactions in the group.

We found that when $S = L$, each species evolved to use a different niche without overlap with the other species. The population of each species was almost completely dominated by the individuals that used the specific niche. As L becomes larger than S , this selection pressure for the convergence became small because there were more redundant niches that could be used without overlap. When $S > L$, several species could evolve to dominate a specific niche while the other remaining species evolved to conflict with each other. Because the latter conflicted species have basically zero fitness, once an individual who could successfully dominate a different niche by chance due to mutations appeared, such an individual quickly occupied the whole population. This maintained the genetic diversity of the conflicted species small. It also should be noted that this change in the niche use of the focal species brought about an occurrence of a new conflict between the focal and the previously dominated species and also allowed another previously conflicted species to dominate a niche. This process sometimes occurred and thus the composition of dominated and conflicted species changed through generations.

In these experiments, there were not clear asymmetric relationships among the species such as the differentiation of the degree of genetic diversity, which could be interpreted as the niche width, among evolving species unlike the clear differentiation of phenotypic plasticity in the original model. In this sense, the coevolution of phenotypic plasticity in competitive interactions for resource use can be a cause of an emergence of asymmetric relationship between species.

4. Conclusion

We discussed the coevolutionary dynamics of the phenotypic plasticity in the context of overlap avoidance behaviors of shared niches in sympatric species. Specifically, we considered whether and how a differentiation of

phenotypic plasticity can emerge under the assumption that there are no initial asymmetric relationships among coevolving species.

We constructed a minimal model where several different species participate in a partitioning of their shared niches, and evolve their behavioral plasticity to avoid an overlap of their niche use. We found the two different types of asymmetric distributions of phenotypic plasticity emerged depending on the settings of the degree of congestion of the shared niches. It should be noted that such a differentiation was not due to the difference in the a-priori setting of the species, but due to the history of the coevolution process of the plasticity. This implies that a dynamic resource partitioning based on a simple trial-and-error itself includes an evolutionary potential to bootstrap such a divergent coevolution process of the phenotypic plasticity. If the degree of congestion of the shared niche space was less congested, one species evolved to be less plastic but all the other species evolved to avoid overlap actively. This corresponds to the emergence of a driver species observed in our previous study (Suzuki et al., 2012). If their shared niche space was congested, one species evolved to avoid overlap actively but all the other species evolved to be less plastic. In both cases, all species tended to obtain the similar amount of fitness regardless of such differences in their plasticity. We also showed that the emerged distributions are coevolutionarily stable in general.

As explained in Introduction, there have been various models on character displacement including evolution of the niche width. It seems not easy to directly compare between our results and those in these related models because we did not assume the evolution of a fixed trait but the evolution of plasticity itself. However, if we assume the axis of the genetically determined phenotypic plasticity as a meta-level niche axis (e.g., the y-axis in Fig. 2) instead of a resource axis, our results show that the character displacement on this plasticity axis can occur without any asymmetric differences among competitive species for their shared resources. In addition, although we focused on the diversity of plasticity rather than the species abundance, the fact that the relationship between S and L can affect the diversification process significantly in our model might reflect discussions on effects of the degree of niche overlap on coexistence of multiple species in the theory of limiting similarity (MacArthur and Levins, 1967; Abrams, 1983; Leimar et al., 2013). In addition, it is interesting that the balance between positive and negative roles of phenotypic plasticity is a key factor for the differentiation of phenotypic plasticity in our model, because it might reflect that the cost

of plasticity is an important factor for the adaptive diversification to occur in (Ackermann and Doebeli, 2004).

There have been various reports on the variation or asymmetry in the plastic responses related to resource use among co-existing species such as temporal avoidance of song overlaps (Ficken and Ficken, 1974) and switching of foraging behaviors (Carnicer et al., 2008) in bird communities, temporal resource partitioning by bats at water holes (Adams and Thibault, 2006), separation of flower-visiting behaviors in time and space among bees and wasps (Rashed and Sherratt, 2007), and morphological changes induced by the coexistence of multiple species in tadpoles (Pfennig and Pfennig, 2012a). Among them, the various biological and environmental factors are expected to be one of the causes of such diversity in plastic responses. On the other hand, our model showed that the diversification of plasticity could emerge without any initial asymmetric properties among competing species. In other words, such a competitive situation for shared resources itself can be a primary factor for the differentiation of plastic responses. We believe that the obtained findings from our minimal model can reflect general aspects of the coevolution process of the phenotypic plasticity in resource use, which are expected to be ubiquitous in many biological, social and artificial systems.

Future work includes the analyses based on different mechanisms of plastic changes in the niche use.

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