



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



Reiji Suzuki*, Takaya Arita

Graduate School of Information Science, Nagoya University, Furo-cho, Chikusa-ku, Nagoya 464-8601, Japan

HIGHLIGHTS

- We model the coevolution of phenotypic plasticity in resource partitioning.
- Several sympatric species participate in a partitioning of their shared niches.
- They evolve their behavioral plasticity to avoid an overlap of their niche use.
- Different asymmetric distributions of plasticity emerged depending on congestion.
- We also show that the emerged distributions are coevolutionarily stable in general.

ARTICLE INFO

Article history:

Received 5 August 2013
Received in revised form
17 February 2014
Accepted 24 February 2014
Available online 4 March 2014

Keywords:

Character displacement
Learning
Multi-species interactions
Agent-based model
Genetic algorithm

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.

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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 (2006)

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, and Kirschel et al. (2009) also reported the character displacement of song (frequency) as well as morphology (bill and body sizes) in African tinker birds. 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 (1980) 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. Various models with relaxed, sophisticated or realistic assumptions have been proposed, investigating the conditions for character

* Corresponding author.

E-mail addresses: reiji@nagoya-u.jp (R. Suzuki), arita@nagoya-u.jp (T. Arita).

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, 2012b). 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 (2009) 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. They showed that the larger maximum flexibility of niche use can promote species diversity under fluctuating environments in general. Ackermann and Doebeli (2004) 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. They showed, both analytically and numerically, that whether the adaptive diversification of resource use composed of several sub-groups 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 partitioning,¹ 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 spectra 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 that 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 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 (1969) pioneering study showed that Wren and Bewick's Wren tended to cycle their song activity with a half-period of about 50 min asynchronously. 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 has been observed in other various species such as frogs (Schwartz and Wells, 1984; Aihara et al., 2014) 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 have 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 and Motro, 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

¹ We 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.

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