Analysis of population structure using individual-based simulation

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博士論文

Analysis of population structure using individual-based simulation
(個体ベースシミュレーションを用いた群集構造の解析)

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Contents

1 General introduction

Adaptive or neutral has been one of a central question in evolutionary ecology. In 1872, John Gulick documented a pattern of diversification of the land snail Achatinella in Hawaii, representing several ecologically equivalent species which undergo parapatric and allopatric distribution (Gulick 1872). This finding led to debates with Alfred Wallace regarding a fundamental question as to whether evolution occurs by natural selection or by chance (Wallace 1888). In the early 20th century, Sewell Wright described Gulick’s pattern as non-adaptive radiation, and considered genetic drift to be its driving mechanism (Wright 1940). This raised serious controversy with Ronald Fisher, who argued that natural selection is the only important evolutionary process (Fisher 1950). And recent years, neutral theory (Hubbell 2000) suggested that stochastic process played an important role for population structure.

However, neutral theory could not express everything, for example, the time change of population structure. The species richness often initially increases, but declines in the later stage, exhibiting “overshooting” (Gavrilets & Vose 2005; Gillespie & Baldwin 2009; Meyer et al. 2010). Overshooting dynamics have been observed in many fossil and extant radiations (Kirchner & Weil 2000; Rohde & Muller 2005; Foote et al. 2007; Powers & Bottjer 2009). These patterns have been regarded as evidence of speciation by adaptive divergence in depauperate environments. However, many examples of explosive radiation lacking any display of ecological or morphological divergence have been known to occur on oceanic islands (Rundell & Price 2009; Gillespie 2004; Holland & Hadfield 2004). This phenomenon of non-adaptive radiation suggests the possibility that processes other than adaptive divergence cause radiation in depauperate environments.

In this study, I constructed individual-based model under the assumption ecological and genetically neutrality, and analyzed the influence of parameters on time change of population structure (Chapter 2).

Although adaptive and non-adaptive radiation provides a contrasting evolutionary patterns, which has been the main driving force in radiation has been discussed for a long time. In theoretical studies, it was mainly based on either of these assumptions (Gavrilets & Vose 2002; Aguiar et al. 2009; Rosindell & Phillimore 2011), there were few models comprehensively handled these two phenomena. In this study, I expanded the model of Chapter 2 and incorporated niche and competition into the model, making it possible to analyze the influence of parameters on the population structure (Chapter 3).

For a long time, diversity of niches is the most crucial factor that creates species diversity. However, recent non-adaptive radiation studies suggested that these are not necessary the case (Gittenberger 1991; Holland & Hadfield 2004; Rundell & Price 2009). In this study, I constructed two types of individual-based habitat models, assuming continuous and discontinuously distributed habitats, and analyzed how these affect species diversity (Chapter 4).

2 Dynamics of evolutionary radiation under ecological neutrality

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2.1 Introduction

The question of whether the dominant driving forces of speciation are stochastic effects or deterministic processes has been a major concern in evolutionary biology. Chance events can play a central role in speciation by polyploidization, hybridization, genetic drift, and founder events / population bottlenecks (Coyne & Orr, 2004). Speciation can occur by mutation and random drift alone, with no contribution from adaptation to environments, as different populations accumulate incompatible genes when there is some geographical isolation (Gavrilets, 2003). Even in several speciation processes involving natural selection, such as Fisher’ s runaway (Lande, 1981) and sexual conflict (Wagner et al., 2012; Chapman et al., 2003), chance plays a major role in the fixation of incompatible alleles in allopatric populations experiencing similar selection processes (mutation-order speciation, which is the evolution of reproductive isolation by genetic drift) (Schluter, 2009). Alternatively, adaptive divergence into different conditions via disruptive selection has been argued as a major process for the evolution of reproductive isolation (Schluter 2000). There is considerable theoretical and empirical support for this ecological speciation model (Rundell & Nosil, 2005; Langerhans et al., 2007; Seehausen, 2006; Melián et al., 2012).

It has generally been accepted that the temporal patterns of speciation are highly connected with the mode of speciation. The explosive radiation observed in the organisms of depauperate environments, such as oceanic islands, crater lakes, and ecosystems after mass extinction, have been thought to be the result of adaptive divergences into an unoccupied habitat. The diversity of unexploited resources stimulates a burst of speciation, with speciation then decelerating as niches become filled. In the fossil record, speciation rates are clearly episodic, accelerating after mass extinction events (Kirchner & Weil, 2000). In addition, species richness often initially increases, but declines in the later stage, exhibiting “overshooting” (Gavrilets & Vose, 2005; Gillespie & Baldwin, 2009; Meyer et al., 2010). Overshooting dynamics have been observed in many fossil and extant radiations (Kirchner & Weil, 2000; Rohde & Muller, 2005; Foote et al. 2007; Powers & Bottjer, 2009).

These patterns have been regarded as evidence of speciation by adaptive divergence in depauperate environments. However, many examples of explosive radiation lacking any display of ecological or morphological divergence have been known to occur on oceanic islands (Rundell & Price, 2009; Gillespie, 2004; Holland & Hadfield, 2004). This phenomenon of non-adaptive radiation suggests the possibility that processes other than adaptive divergence cause radiation in depauperate environments.

Stochastic processes have not been considered to accelerate speciation in depauperate environments. Theoretical analyses have suggested that population size does not affect the speciation rate when the dominant driving force for speciation is genetic drift (Orr & Orr, 1996). However, recent analyses of the models incorporating neutral metacommunity dynamics document that the metacommunity size affects the evolutionary pattern (Rosindell & Phillimore, 2011). If species richness is positively correlated with the metacommunity size as is expected in neutral community models, the speciation rate may also be positively correlated with the metacommunity size. Lineages in depauperate environments should have a relatively larger metacommunity size than those in species-rich environments. This leads to the expectation that the speciation rate may increase in depauperate environments without speciation by adaptive divergence into different niches. This hypothesis was tested in a model considering only neutral mutation, genetic drift, reproductive incompatibility, and neutral community dynamics. A model with minimal assumptions was introduced for speciation. In recent studies, some neutral models were used in the speciation model (Aguiar et al., 2009; Rosindell et al., 2010; Rosindell & Phillimore, 2011). Community dynamics and species diversity patterns were described by instantaneous speciation using a point mutation model (Hubbell, 2001; Brideau et al., 2006; Bomblies et al., 2007). Diversity patterns caused by neutral processes were also described by a more realistic model, i.e., the protracted speciation model (Rosindell et al., 2010). In this model, speciation occurs in a gradual manner, and top-down processes and temporal dynamics of genetic variations and radiation are ignored. Levels of genetic variations affect speciation rates and patterns of radiation (Fine 2015). Incorporating effects of genetic variations within populations is essential to describe temporal changes in speciation rates. Thus, we assumed that the Dobzhansky-Muller incompatibilities (Dobzhansky, 1937; Muller, 1942) between alleles accumulate in different lineages by random mutation, genetic drift and isolation by distance.

2.2 Methods

In the present study, ecologically neutral population and community dynamics were incorporated in the system by introducing a spatially implicit individual-based stochastic patch occupancy model similar to other neutral models (Hubbell, 2001). We assumed a uniform island (metacommunity) comprised of an M number of patches. A species colonizes from elsewhere on the island and constitutes a population with an N number of individuals ($N \leq M$). The dynamics of speciation, extinction and species richness were observed in the simulation. N is invariant throughout the single simulation.

The hypothetical island was indicated by a two-dimensional square lattice with an M number of grid cells (number of the cells per one side is q), each of which denotes a habitat patch. A patch is defined as a continuous area of habitat. Each patch can be unoccupied or occupied by a single individual. The island area is defined by the total area of the M number of cells ($M = q^2$) that are connected with each other via one of their eight neighboring cells.

Each patch is either occupied by one individual or empty. Each individual mates with another conspecific individual that resides within a particular range centered on the individual. Every individual dies after reproduction, and the patches they occupied become empty or occupied by either their offspring or the offspring of other parents. The offspring disperse within a particular distance in a particular probability, and occupy the patches that they reach. The total number of individuals is assumed to be the same through each time unit (zero-sum dynamics), and all individuals of all species are ecologically identical. In this individual-based ecologically neutral model, each individual is assumed to be diploid and hermaphroditic, and its fitness is constant regardless of the differences in species. Each time unit is assumed to experience four steps: reproduction, dispersal, mutation, and speciation. We repeated this process for 1000 or 2000 time units and observed the dynamics of the population (Fig. 1).

2.2.1 Genes, mating, and speciation

The Dobzhansky-Muller (DM) model has been used in a number of studies in different forms (Orr & Turelli, 2000). The DM model extended to the most general form contains multiple alleles at each n loci system (Gavrilets, 2003), in which each genotype has a survival rate of either 0 or 1 at random. Another version of the DM model that is commonly used has two alleles at each n loci system (Orr & Orr, 1996; Gavrilets & Hai, 1998), assuming that hybrid incompatibility arises only when the accumulation of between-loci incompatibility exceeds a threshold. In the present study, we first used the latter model for simplicity. First we assumed that there was no gradient in the inviable rate (DM1). Next, we incorporated a gradual increase in hybrid incompatibility with an increase in between-locus incompatibility into the above model (DM2). If there is a complete reproductive incompatibility between the individuals, these individuals are defined as different species.

Each individual (diploid and hermaphrodite) is assumed to possess genes of two alleles (0 or 1 allele) at each n loci system. Initially, an N number of individuals of a single species that possess an identical genotype fixed by allele 0 was randomly placed in the grid cells. This situation denotes that a species colonized from the mainland to the island spreads to the whole area of the island within a fairly short time. A new, derived allele is incompatible with an ancestral allele at some other locus, or with a derived allele at another locus. Similar to former Dobzhansky-Muller models, we assume that the separate incompatibilities between loci contribute additively to a breakdown score that determines the hybrid incompatibility. Hybrids become inviable when their breakdown score reaches a threshold value, h. We suppose that a hybrid genotype suffers k distinct incompatibilities and that the ith incompatibility contributes c_i to the breakdown score; $c_i = 1$ when isolation was fixed (00 and 11), otherwise $c_i = 0$. The survival rate of this genotype is $W = f(\sum_{i=1}^{k} c_i)$, where f denotes the function that translates the breakdown score to survival rate. For simplicity, we designated two simple forms for the function f with minimum assumption. In the first model (DM1), we assume binomial survival rate, where $W = 1$ if $h \geq \sum_{i=1}^{k} c_i$, and otherwise $W = 0$. In the second model (DM2), we assume $W = 1 - (\sum_{i=1}^{k} c_i/h)^2$ if $h \geq \sum_{i=1}^{k} c_i$, and otherwise $W = 0$. In this case, the survival rate decreases non-linearly with increasing between-loci incompatibilities. A single offspring was produced for each reproduction with the probability W. Only at this point was the neutral assumption not considered in this model. The offspring receives a one-half complement of alleles from each parent. A mutation (from 0 to 1, or 1 to 0) occurs at each locus, with the probability of u for each time step. Unlike a typical DM model, our model allowed for two-way mutation. Although this assumption could cause breakdown of reproductive isolation, if μ is sufficiently low and L, which is defined by the length of allele sequence, is long, this probability can be ignored, such as in actual genes. The diversity patterns were also examined when speciation was assumed to occur as a point mutation process (Brideau et al., 2006). Under the point mutation model, a particular individual randomly selected from the population instantaneously became a new species.

2.2.2 Reproduction and dispersal

An individual approaching reproduction chooses its mate within a 3×3 square with the center at the individual’ s patch. We assumed that the individual is more likely to mate with a neighbor than with an individual dwelling far away. In this model, mating occurs only between the individuals occupying neighborhood patches. If no conspecific individuals occupied neighborhood patches within the 3×3

square, and therefore, there was no mate within its range, the area for choosing a mate was extended recursively until it included a mate within the range. An offspring was produced for each reproduction and it occupied the center patch of the 3×3 square. In the case of DM2, mating pairs were chosen from the conspecific neighbors with the probability determined by the hybrid incompatibility between these two individuals. An individual was randomly selected from the offspring produced by these mating pairs and was placed in the central patch of the 3×3 square. This process was repeated in all 3×3 squares existing in the hypothetical island. Because of spatial aggregation of conspecific individuals, mating pair was found within the 3×3 square in most cases, and the area for choosing a mate was rarely extended in our simulation of both DM1 and DM2 (Fig. 1). Even if the area was extended, it was never extended to 7×7 square. Therefore, this assumption does not affect the effects of isolation by distance.

In terms of the dispersal process, after all offspring were placed, offspring selected at random were moved to any of the eight neighborhood patches at random. If another offspring already occupied that patch, the locations of the two individuals were exchanged. The selection of individuals for dispersal was conducted $N \times d$ times with a dispersal probability of d. The actual dispersal probability is higher than d because locations of the two individuals are exchanged when the destination patch is occupied.

The reproduction process was repeated until the number of offspring reached N, and then all of the individuals of the previous time unit were eliminated. Thus, the total number of individuals N was kept constant through time.

2.3 Results

2.3.1 Diversity dynamics

The results of the simulation showed that the speciation rate per species per unit of time rapidly increased after colonization and reached a peak (Fig. 2). At equilibrium, the speciation rate was close to zero. The extinction rate also showed the phases of an increase, peak, and gradual decline. Thus, at equilibrium, the community reached a steady state with a very low speciation and extinction rate. This pattern differed from that created using point mutation and protracted speciation models (Hubbell, 2001; Rosindell et al., 2010), which showed no decrease in the speciation and extinction rates at equilibrium and no overshooting dynamics of species richness. The dynamics of species richness during radiation exhibited a pattern of overshooting with an initial phase of exponential increase followed by a slower decline (Fig. 3). Both speciation models (DM1 and DM2) generated a consistent temporal pattern of species richness. When the ratio of the length of each allele sequence (L) versus the reproductive isolation threshold (h) was constant, the temporal patterns of species richness differed depending on the values of L. The overshooting peak of species richness became higher when L was larger. In contrast, the values of L generally showed no effect on the equilibrium species richness. The differences in mutation rates (μ) affected the temporal patterns of species richness. The overshooting of species richness occurred only under moderate levels of mutation rates, and no overshooting was observed when the mutation rate was either extremely high or low (Fig. 4).

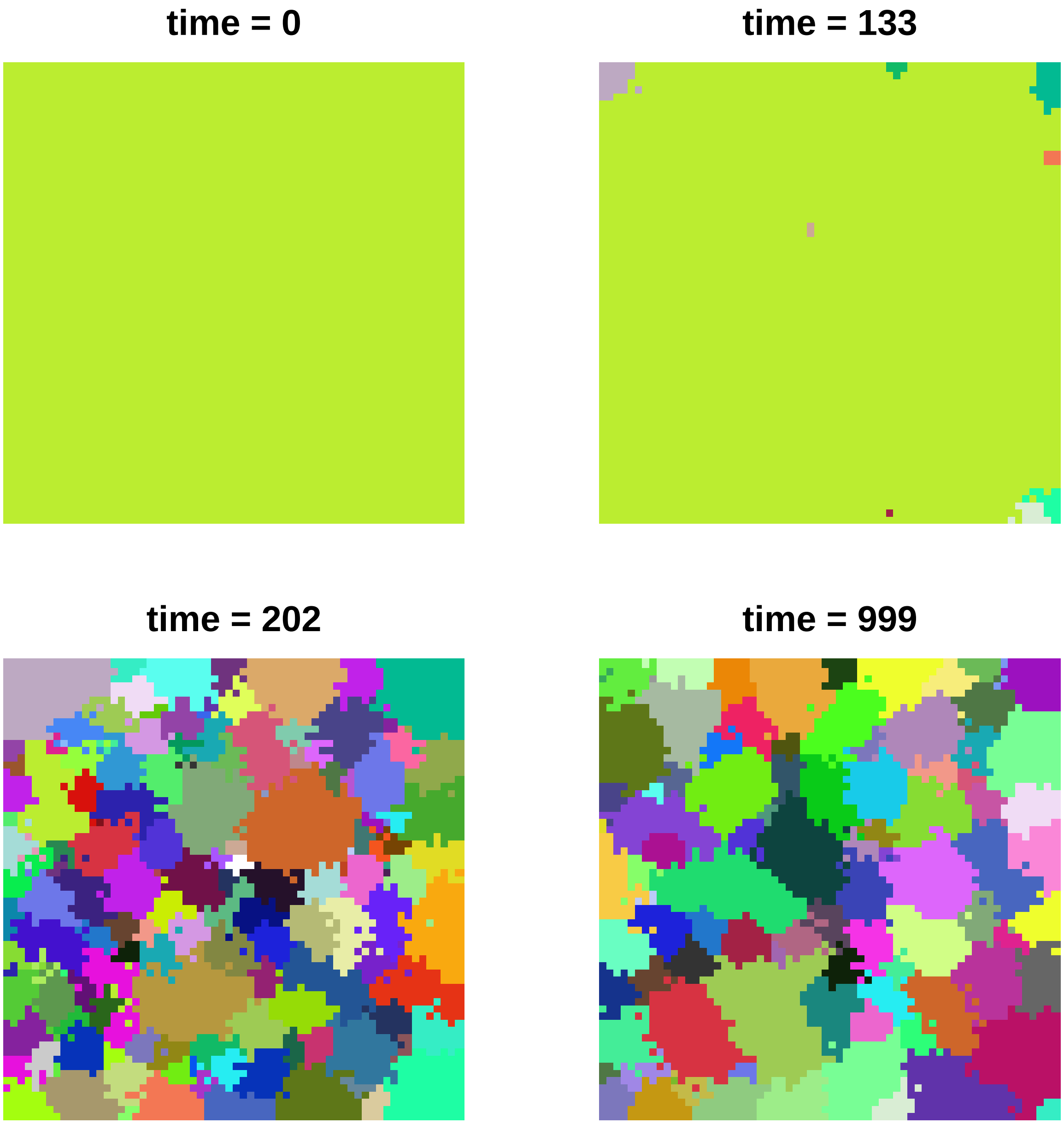

Fig. 1: A representative example of a DM1 simulation. A cell means a individual, and different species are indicated by different colors. $Area = 4096$ (64×64), loci length = 512, reproductive isolation threshold = 16, mutation rate = 0.001, dispersal probability = 0.15. In the initial stage of the simulation, all individuals belong to the same species (lime green cells). After 202 time steps (t = 202), species richness reaches its highest value, exhibiting an overshooting pattern. After the peak, species richness decreases and reaches an equilibrium.

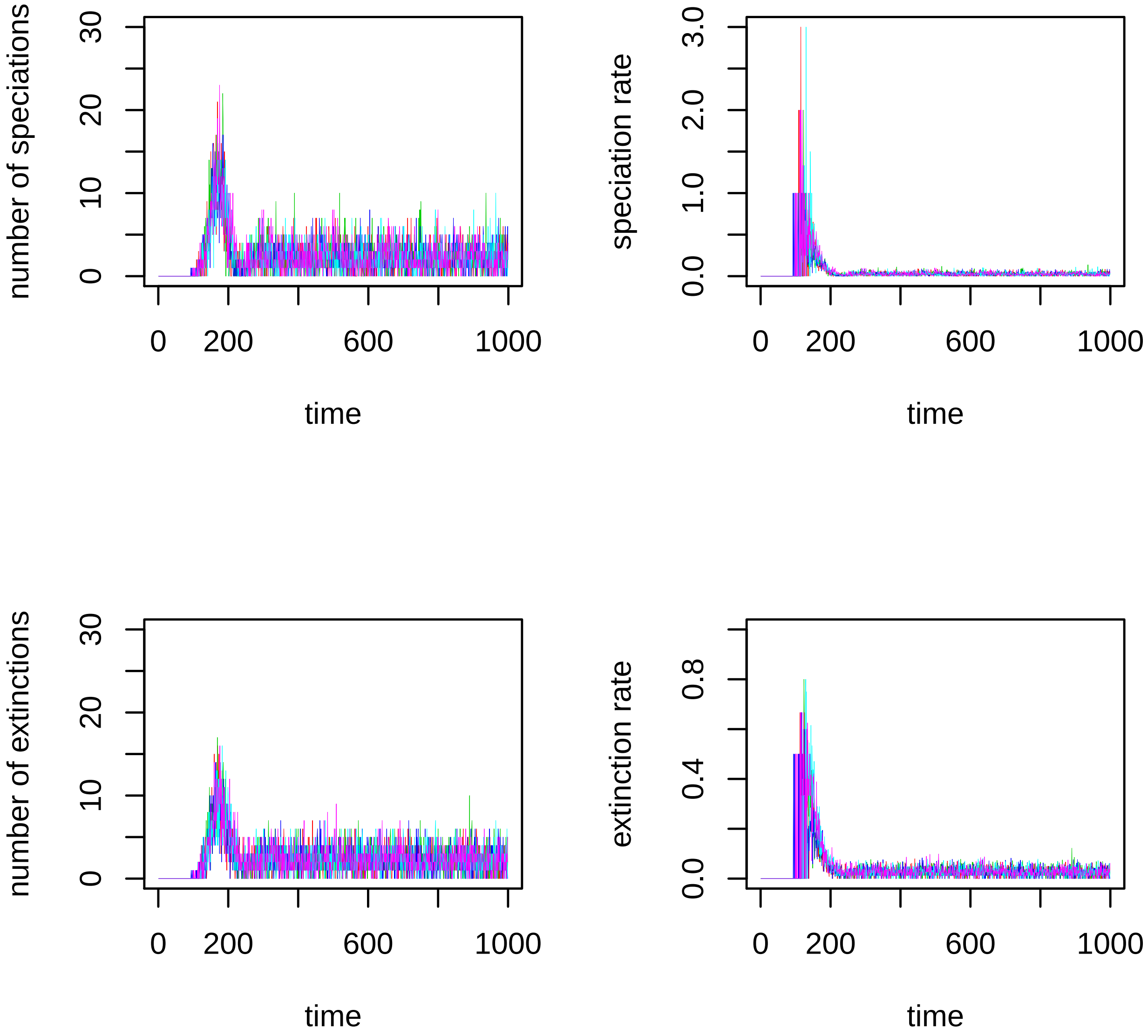

Fig. 2: The number of speciations and extinctions and their rate per species. All parameters are the same as those in Fig. 1. Each simulation was repeated 5 times. Each color represents one trial. Each parameter reached a peak after stagnation and then decreased to zero.

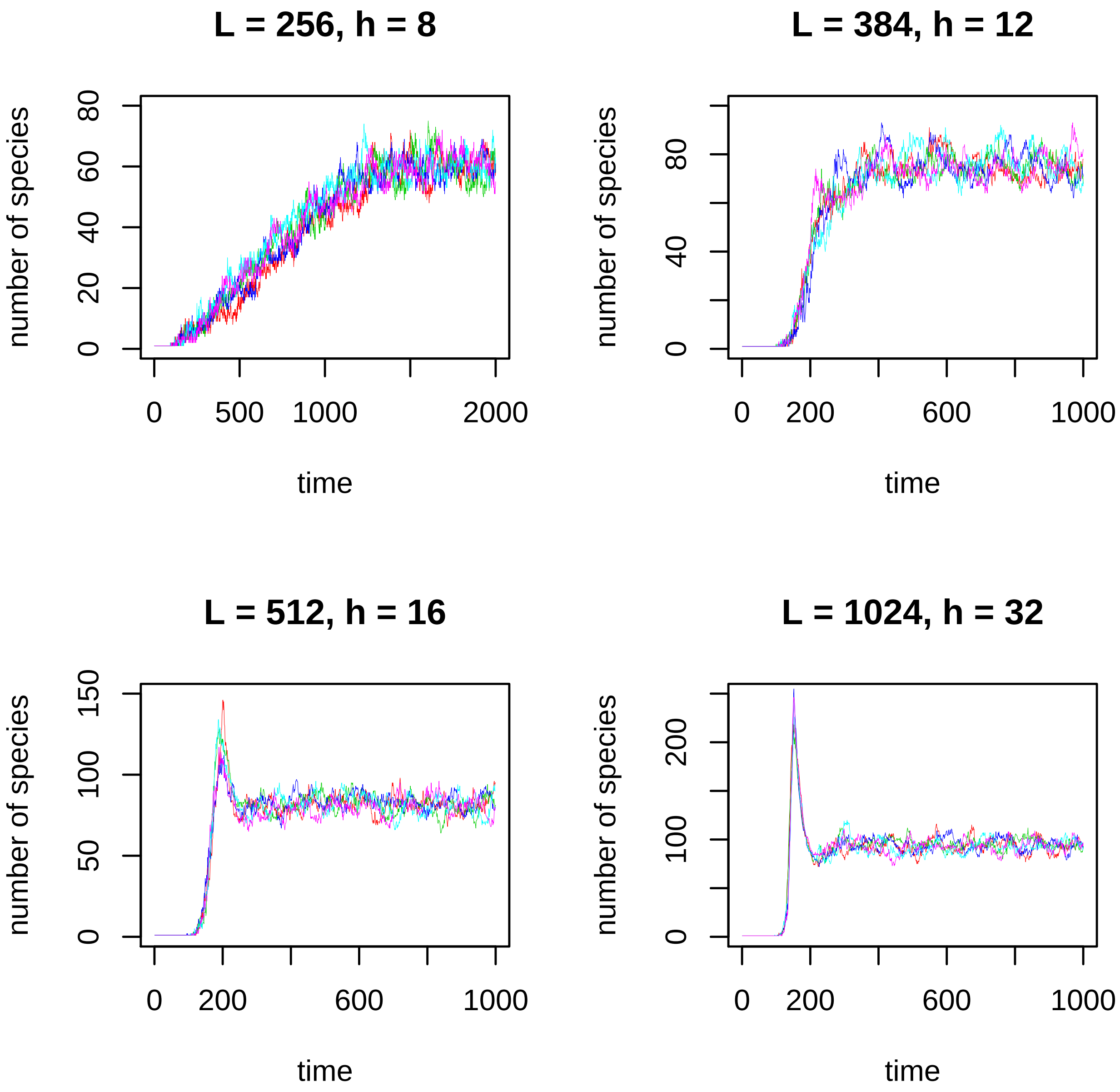

Fig. 3: Temporal patterns of species richness when the ratio of the length of each allele sequence (L) versus the reproductive isolation threshold (h) was held constant. Each simulation was repeated 5 times. Each color represents one trial. The peak of species richness becomes unclear when the length of the allele sequence is moderate. The other parameters are the same as those in Fig. 1.

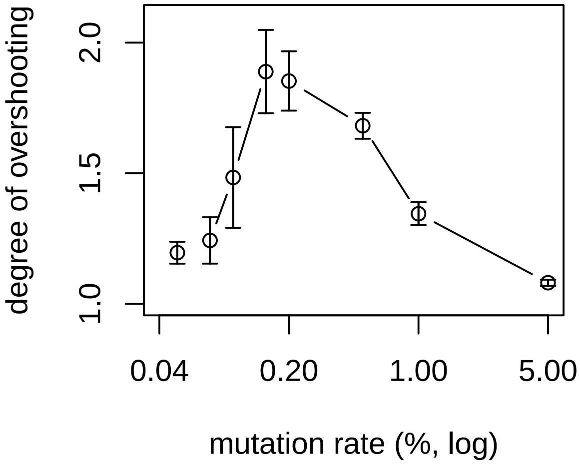

Fig. 4: The ratio of species richness between the peak and equilibrium. The error bars show the 95 % confidence interval. The equilibrium was defined as the average of the last 100 time units (900-999), and the peak was regarded as the maximum number of species in the trial, i.e., it did not necessarily correspond to the overshooting peak. These values were calculated based on an average of 5 time trials. The height of the peak relative to the equilibrium species richness becomes low when the mutation rate was either extremely high or low. The other parameters are the same as those in Fig. 1.

2.3.2 Genetic variation

The levels of genetic variation within populations were associated with the speciation rates of the population. The species with higher genetic variation tended to exhibit higher speciation rates than those with lower genetic variation. The temporal changes in genetic variation within a species showed a consistent relationship with the radiation dynamics. For example, in the initial stage of the simulation, speciation did not occur until genetic variation accumulated in the population through mutation. In addition, the mean genetic variation of the species reached a maximum just before the radiation occurred, and decreased after the overshooting phase (Fig. 5).

2.3.3 Community structure

Similar to other neutral models, the present model showed that the island area has a positive effect on species richness. When the population density (N/M) is constant, both M and N are positively correlated with the speciation rate at the burst stage and the equilibrium species richness (Fig. 6).

Species rank abundance curves, in which the proportional abundance of the species was plotted against their abundance rank, showed a log-normal relationship at equilibrium (Fig. 7). This was consistent with the results of other neutral community models. The curve showed a geometric series at

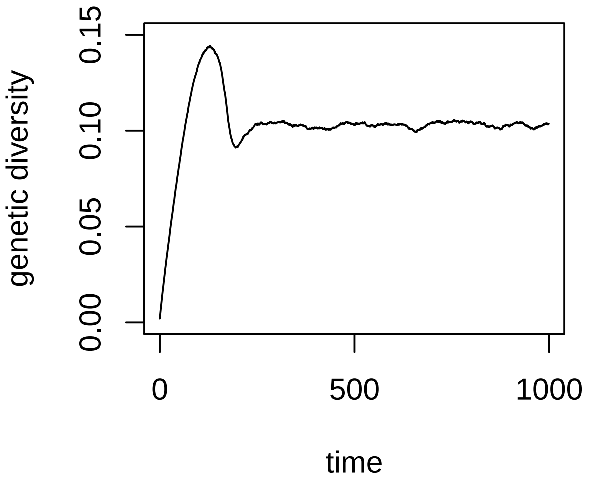

Fig. 5: Genetic diversity in the population. The level of genetic diversity is defined as an average of heterozygosity among all loci of all individuals. The values of the parameters used are the same as those in Fig. 1.

the initial stage of radiation, whereas it exhibited a log-normal trend at equilibrium. This corresponded to the expectation that species' abundances conform to a geometric series during early succession, but approach a log-normal series as the community ages (Whittaker, 1972).

2.4 Discussion

The results of the simulation suggest that the pattern of speciation burst typically observed in organisms in depauperate environments can occur under conditions of neutrality. The accelerated speciation in the initial stage of radiation and the subsequent decline in speciation can be explained without assuming the existence of vacant niches and interspecific competition. The present simulation suggests that there are four phases in this radiation. In the first phase, mutation is accumulated with no speciation. This explains the presence of a time lag between a mass extinction event and the subsequent radiation that is observed in the fossil record (Kirchner & Weil, 2000). Second, synchronized speciation occurs, which causes fragmentation of the population. For relatively small populations of species susceptible to genetic drift, the genetic diversity of the entire population and speciation rate exhibit decreasing trends (phase 3) (Fig. 2, Fig. 5). Finally, the speciation rate and extinction rate are balanced and approach zero, reaching equilibrium (Fig. 2). This pattern of dynamics represents a genetic mechanism that was not observed in the previous speciation models, such as the point mutation model (Hubbell, 2001) and protracted speciation model (Rosindell et al., 2010).

In this study, we do not clearly define time scales. The overshooting reaches a maximum value in the middle of the mutation rate (Fig. 4), and high values of L and h increase the degree of

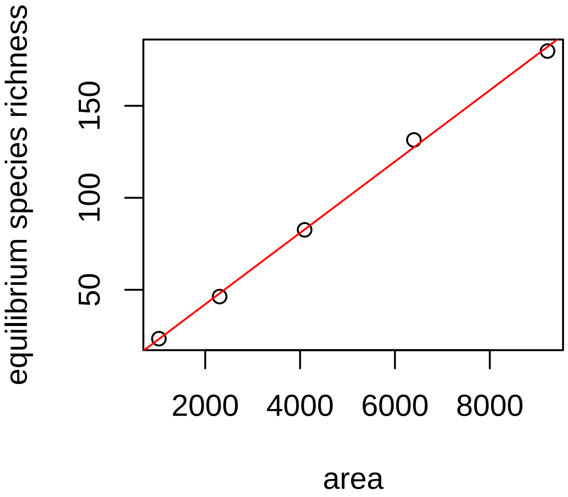

Fig. 6: The relationship between area and species richness. Each value was calculated based on the average of the last 100 values of the trial. The initial values of the parameters used are the same as those in Fig. 1, except for "area".

overshooting (Fig. 3), suggesting that the results can be extended to a wide range of time scales. Indeed, overshooting dynamics of species diversity have been observed in datasets with time scales ranging from a few million years, in the case of Cenozoic molluscan fossils (Foote et al. 2007), to even 10 days, in the case of laboratory experiments using microorganisms (Meyer et al. 2010).

The positive correlation between the speciation rate and population size is the major cause for the accelerated speciation in the initial stage of radiation and the subsequent decline in speciation because the population size of each species should decrease with increasing species richness. Given that immigrants to fairly large oceanic islands, such as Hawaii, have a much higher population size than their mainland relatives because of the lower species richness and absence of predators, the above findings suggest that explosive radiation is likely to occur on such large oceanic islands. The explosive radiation often observed on large oceanic islands and ancient lakes might be the result of the increasing population size of the initial populations (Seehausen, 2006; Gillespie, 2004).

The present study suggests that the variety of characteristics of radiation in depauperate environments can be explained by neutral processes without considering the processes of adaptive divergence into vacant niches. Radical changes in the divergence rate and community structure are documented under a stochastic null model (Hubbell, 2001). These findings do not refute the role of adaptive divergence in speciation. Ecological speciation is common, particularly on oceanic islands, and the same patterns observed in this study also arise through ecological speciation (Gavrilets & Vose, 2005). However, our model shows that the assumption of the ecological processes of speciation and empty ecological niches, which has been adopted in most models of adaptive radiation, are not required to explain the dynamics of overshooting species richness followed by declining speciation and extinction rate.

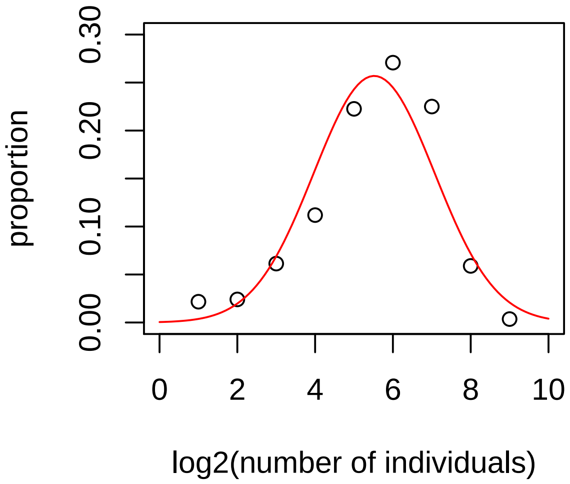

Fig. 7: The community structure at equilibrium (time=999), displaying the distribution of the number of species of an individual class. The values are calculated from ten time trials, and the initial parameters are the same as those in Fig. 1. The results are consistent to the lognormal-distribution of rare species, suggesting underestimation (Hubbell, 2001).

However, our neutral model cannot reproduce the large changes of species richness after equilibration, which may occur as a result of immigration of ecologically effective species from other regions (Knops et al., 1999), and intermittent species richness increasing due to niche expansion (Seehausen, 2006). If such patterns are observed, it can be stated that the effect of non-neutrality is working. Our study suggests that speciation is strongly affected by metacommunity dynamics as well as metapopulation dynamics. Large metapopulation and metacommunity sizes are essential for promoting radiation and enhancing species diversity.

3 Adaptive and non-adaptive radiation as alternative states in radiation

3.1 Introduction

In 1872, John Gulick documented a pattern of diversification of the land snail Achatinella in Hawaii, representing several ecologically equivalent species which undergo parapatric and allopatric distribution (Gulick, 1872). This finding led to debates with Alfred Wallace regarding a fundamental question as to whether evolution occurs by natural selection or by chance (Wallace 1888). In the early 20th century, Sewell Wright described Gulick’ s pattern as non-adaptive radiation, and considered genetic drift to be its driving mechanism (Wright 1940). This raised serious controversy with Ronald Fisher, who argued that natural selection is the only important evolutionary process (Fisher 1950). Thereafter, a number of studies have been conducted to investigate the process of non-adaptive radiation and the causes of its differences from adaptive radiation, a pattern of multiplication of species accompanying niche diversification.

There are three major hypotheses for processes that yield differences between the patterns of adaptive and non-adaptive radiation. First, natural selection may dominate in the former but non-adaptive processes in the latter (Wilke, Benke, Brändle, Albrecht & Bichain, 2010; Wellenreuther & Sánchez-Guillén, 2016). Despite more than 100 years of arguments, there is little evidence to support this traditional hypothesis. Second, non-adaptive radiation may occur when species are strongly constrained by ecological saturation (Rowe, Aplin, Baverstock & Moritz, 2011) or by niche conservatism (Kozak, Larson, Bonett & Harmon, 2005) and when parapatric and allopatric species are isolated by competitive interaction (Gittenberger, 1991). Although this is plausible, non-adaptive radiation is also observed in unsaturated ecosystems such as Hawaii and other oceanic islands (Holland & Hadfield, 2004; Rundell & Price, 2009). In addition, the same lineages often show both adaptive and non-adaptive radiation in different areas of the same islands (Gillespie, 2004; Wada & Chiba, 2013). Finally, adaptive radiation may occur after a period of non-adaptive radiation by migration of species and subsequent character displacement between sympatric species (Rundell & Price, 2011). However, it is known that the same lineages exhibit both non-adaptive radiation continuing for a long time and adaptive radiation occurring within a short time (Gillespie, 2004). There is no evidence regarding the evolution of species from generalist to specialist (Schluter, 2000), suggesting that the level of divergence of niches has no relationship with time (Kassen, 2002). Thus, it remains unclear what causes the differences between these types of radiation.

A number of models have been developed for adaptive radiation (Gavrilets & Vose, 2002; Gavrilets & Vose, 2009) and radiation of neutral species (Aguiar, Baranger, Baptestini, Kaufman, Bar-Yam, 2009; Rosindell & Phillimore, 2011), but little attention has been placed on models considering both adaptive and non-adaptive radiation. In order to estimate factors that change radiation to adaptive or non-adaptive, we introduced a spatially implicit individual-based stochastic patch occupancy model. Its basic framework is the model used in our previous study (Suzuki & Chiba, 2016) that assumes zero-sum community dynamics and an island (metacommunity) comprising M number of patches.

Initially, a species colonises from elsewhere on the island and establishes a population with N number of diploid and hermaphrodite individuals ($N \leq M$). As in our previous model, we assumed that Dobzhansky - Muller incompatibilities between alleles accumulate in different lineages by random mutation, genetic drift and isolation by distance. We modified our previous model by introducing phenotypic values determined by genotypic values of the loci which we considered. Different habitat conditions (habitat values) were randomly assigned to each patch, and the fitness of each individual was determined by the degree of coincidence between the habitat and phenotypic values.

In addition to speciation by geographical isolation, speciation may also occur as by-product of adaptation to different environments if ecological and reproductive traits are linked. This ecological speciation was accounted for in our model by assuming positive correlation between the difference in phenotypic value and the level of reproductive isolation.

3.2 Methods

3.2.1 Structure of the model

In this study, a spatially implicit individual-based stochastic patch occupancy model was constructed. The basic structure of the model is the same as the model used by our previous study (Suzuki & Chiba). We assumed an island (metacommunity) comprised of M number of patches. A species colonises from elsewhere on the island and establishes a population with N number of individuals ($N \leq M$). N is invariant throughout the single simulation. The hypothetical island was represented by a two-dimensional square lattice with M number of grid cells, each of which denotes a habitat patch. A patch is defined as a continuous area of habitat. Each patch can be unoccupied or occupied by a single individual, and has niche parameter k of random value ($k = 0, 1, \ldots, K$). It is invariant during the single simulation.

In this individual-based model, each individual is assumed to be diploid and hermaphroditic. An individual has two sets of genes that relate to incompatibilities in reproduction and to phenotypic values, respectively. Each time unit is assumed to comprise four steps: reproduction, dispersal, mutation and speciation. In each generation, each individual moves to another patch at random within a range of a circle with radius D. Each individual mates with another conspecific individual that resides within a particular range centred on the individual. Every individual dies after reproduction, and the patches they occupied become empty or occupied by either their offspring or the offspring of other parents. The offspring disperse within a particular distance in a particular probability, and occupy the patches that they reach. The total number of individuals is assumed to be the same through each time unit (zero-sum dynamics). We repeated this process for 1000 time units and observed the dynamics of the population.

3.2.2 Genes, mating and speciation

The Dobzhansky - Muller (DM) model has been used in several studies in different forms to explain the process of speciation (Orr & Threlli, 2001). The DM model reduced to its most general form contains multiple alleles at each n loci system (Gavrilets, 2003), in which each locus has a survival rate of either 0 or 1 at random. Another version of the DM model that is commonly used has two alleles at each n loci system (Orr & Orr, 1996; Gavrilets & Hai, 1998), assuming that hybrid incompatibility arises only when the accumulation of between-loci incompatibility exceeds a threshold. In this study, we used the latter model for simplicity. We assumed that there was no gradient in the inviable rate. If there is a complete reproductive incompatibility between individuals, these individuals are defined as different species. Details of this DM model were shown by our previous research (Suzuki & Chiba, 2016).

Each individual (diploid and hermaphrodite) is assumed to possess genes of two alleles (0 or 1 allele) at each locus. Initially, N number of individuals of a single species that possess an identical genotype fixed by allele 0 are randomly placed in the grid cells. This situation denotes that a species colonising the island from the mainland spreads to the whole area of the island within a fairly short time. A new, derived allele is incompatible with an ancestral allele or a derived allele at another locus. Similar to former Dobzhansky - Muller models, we assume that separate incompatibilities between loci contribute additively to a breakdown score that determines hybrid incompatibility. Hybrids become inviable when their breakdown score reaches a threshold value, h. We suppose that a hybrid genotype suffers k distinct incompatibilities and that the ith incompatibility contributes c_i to the breakdown score; $c_i = 1$ when isolation was fixed (00 and 11), otherwise $c_i = 0$. The survival rate of this genotype is $W_m = f(\sum_{i=1}^{k} c_i)$, where f denotes the function that translates the breakdown score to survival rate. For simplicity, we designated a simple form for the function f with minimum assumption. In this model, we assume binomial survival rate, where $W_m = 1$ if $h \geq \sum_{i=1}^{k} c_i$, and otherwise $W_m = 0$. A single offspring was produced for each reproduction event with the probability W_m. Each individual is also assumed to possess genes that determine phenotypes. Phenotype value (H) was assigned by the number of loci that possess the allele "1" as homozygote. The offspring receives one half of its complement of alleles from each parent. A mutation (from 0 to 1, or 1 to 0) occurs at each locus, with the probability of μ for each time step. Unlike a typical DM model, our model allowed for two-way mutation. Although this assumption could cause breakdown of reproductive isolation, if μ is sufficiently low and L, which is defined by the length of allele sequence, is long, this probability can be ignored, such as in actual genes.

3.2.3 Reproduction, dispersal and competition

Reproducing individuals choose their conspecific mating partners randomly within a circle of radius D with its centre at patch j. Each individual mates only once. Individuals to oviposit are selected at random 30 times, allowing duplication from the individuals within the circle. A single offspring is produced for each oviposition. Adaptability (W_h) of each individual for each patch is expressed by the difference between phenotype value (H) of the individual and niche parameter (k) of the patch, therefore, $W_h = 1 - |k - H|/K$. After reproduction, the individual occupying the patch j is replaced by the individual that has the highest W_h among the offspring produced by all of the species within the circle with its centre at patch j, and this process is repeated for all occupied patches. In terms of the dispersal process, an individual selected at random from the offspring of the individual sitting in the patch j moves to another patch selected at random within the circle of radius D with its centre at patch j. If another individual already occupies that patch, the patch of the occupant is exchanged with the patch of the disperser. This process is also repeated for all patches.

3.2.4 Characteristics of species

Frequency distribution of phenotype value (H) and parameters of the niches occupied by conspecific individuals are examined for each species. Mean phenotype of a species is obtained as the mean of H among the individuals of the species. Phenotypic variability of a species is expressed by standard deviation of H. Level of specialisation of a species is expressed by mean adaptability (W_h) among conspecific individuals. Species richness was examined in different spatial scales. Average of local richness (alpha diversity) was obtained in 3×3 patch areas, and total richness was examined in the whole community (gamma diversity).

3.2.5 Ecological Speciation

In order to verify the robustness of the model, we introduced an ecological speciation model as an alternative of the speciation model by geographical isolation and genetic drift. This model assumes that differences in ecological traits (phenotypes) cause reproductive isolation. Fitness of offspring is determined by similarity of phenotypes between their parents. In reproductive process, offspring are removed stochastically from the population with probability of $1 - (|H_i - H_j|/K)^p$, where H_i and H_j indicate phenotype value of the parents (phenotype of the individual i and j), and indicates strength of reproductive isolation. This means that reproductive success between individuals decreases with increase of ecological (phenotypic) difference between them.

3.2.6 Neutral model

We consider also a model under neutral assumption. In this model, death or survive of each offspring is determined at random. This model is same as our previous neutral model (Suzuki & Chiba, 2016).

3.3 Results

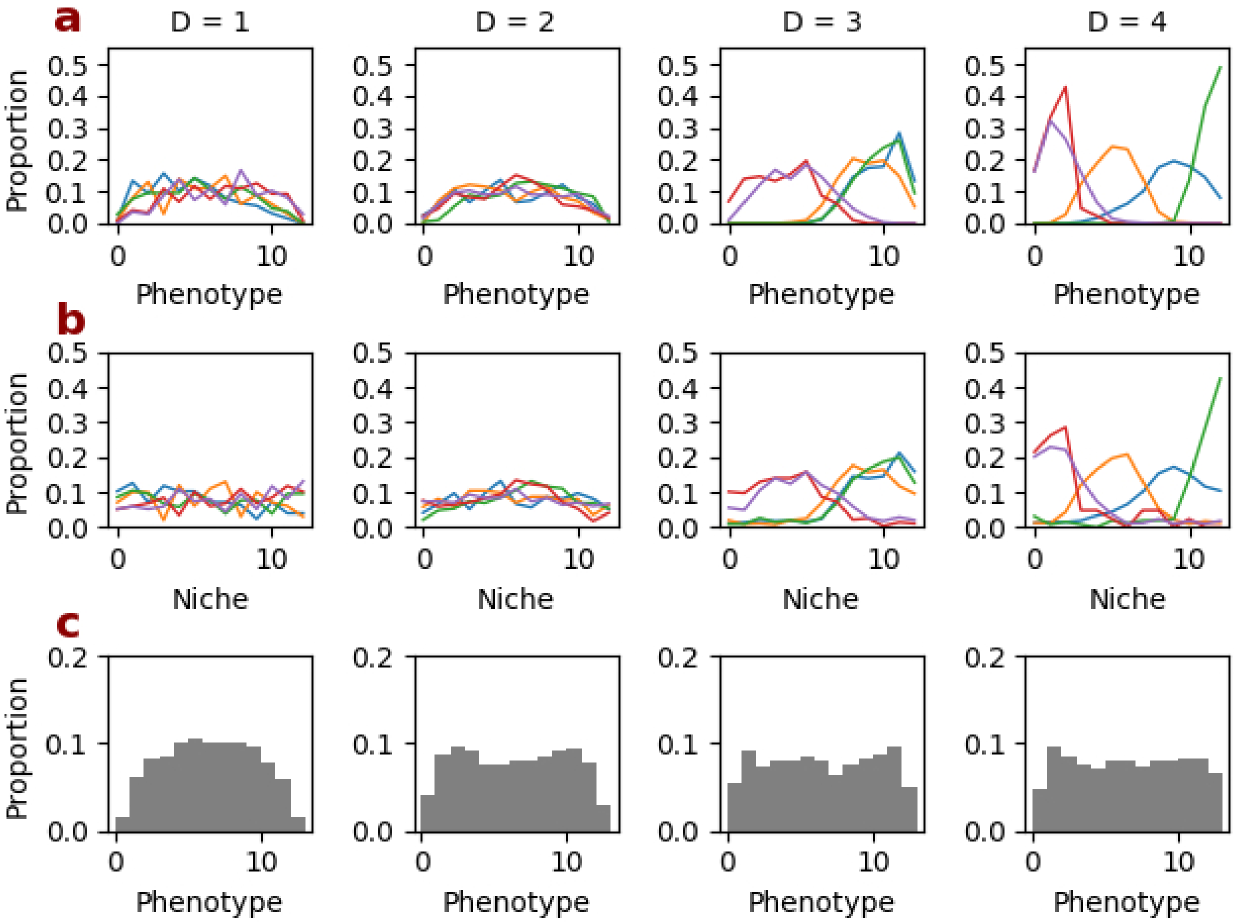

Fig. 1: Frequency distribution of phenotype (a) and niches occupied (b) by each of the five most dominant species at equilibrium. Different species are shown in different colors. Frequency distribution of phenotypes in total species is also shown (c). Patterns under different dispersal rates (D) are shown.

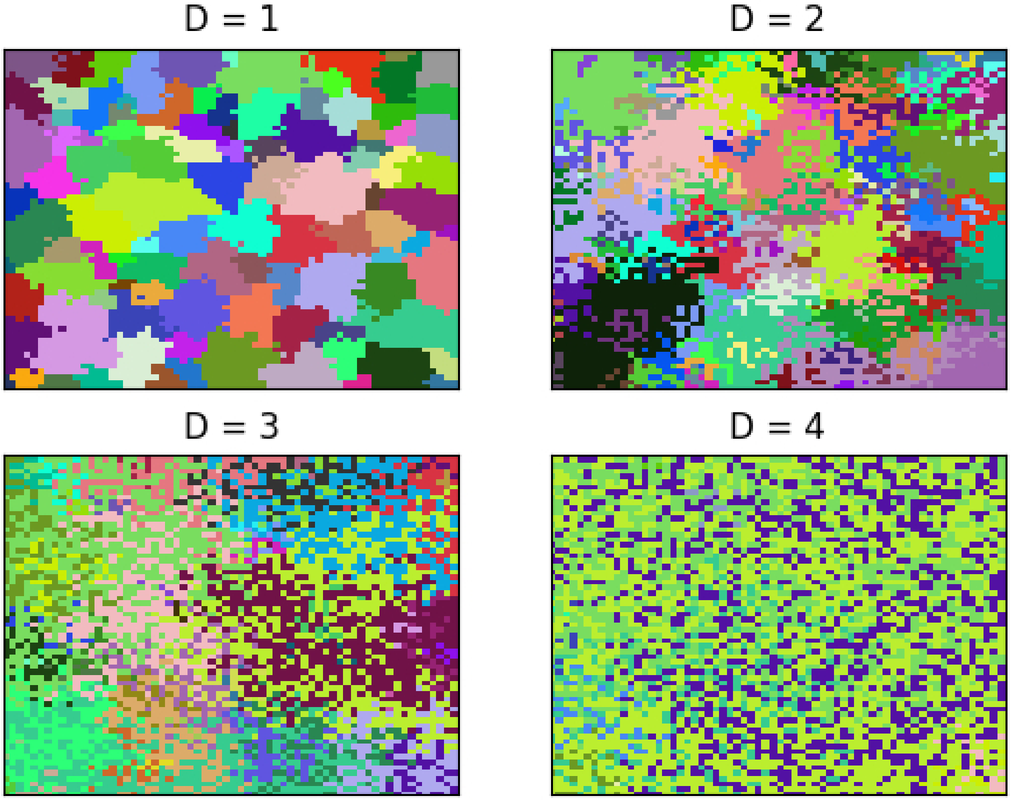

Fig. 2: Geographical patterns of the distribution of species. Individuals of different species are shown in different colors. Patterns under different dispersal rates (D) are shown.

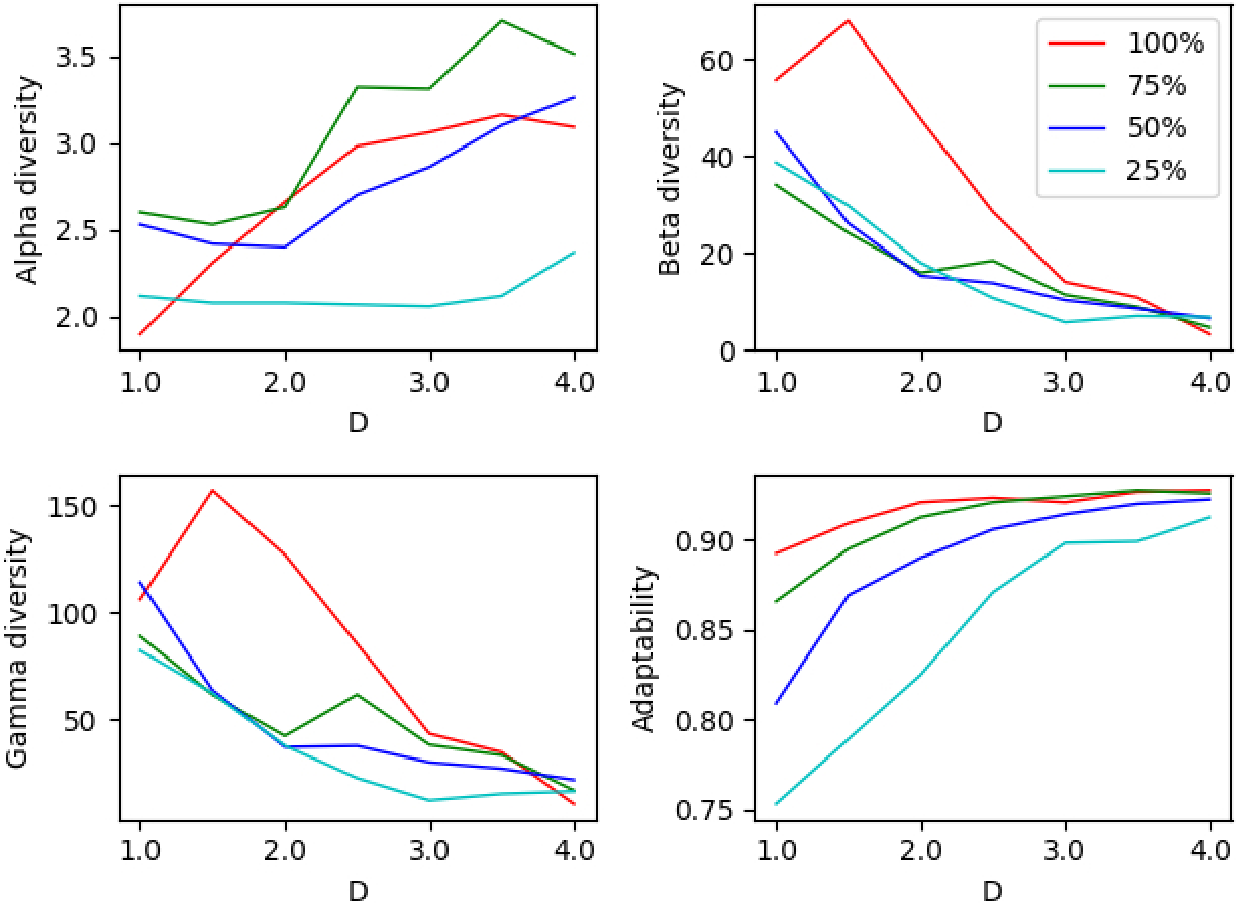

Fig. 3: Relationships between species richness (alpha, beta and gamma) and dispersal rate. The relationship between adaptability (level of specialisation) and dispersal rate is also shown.

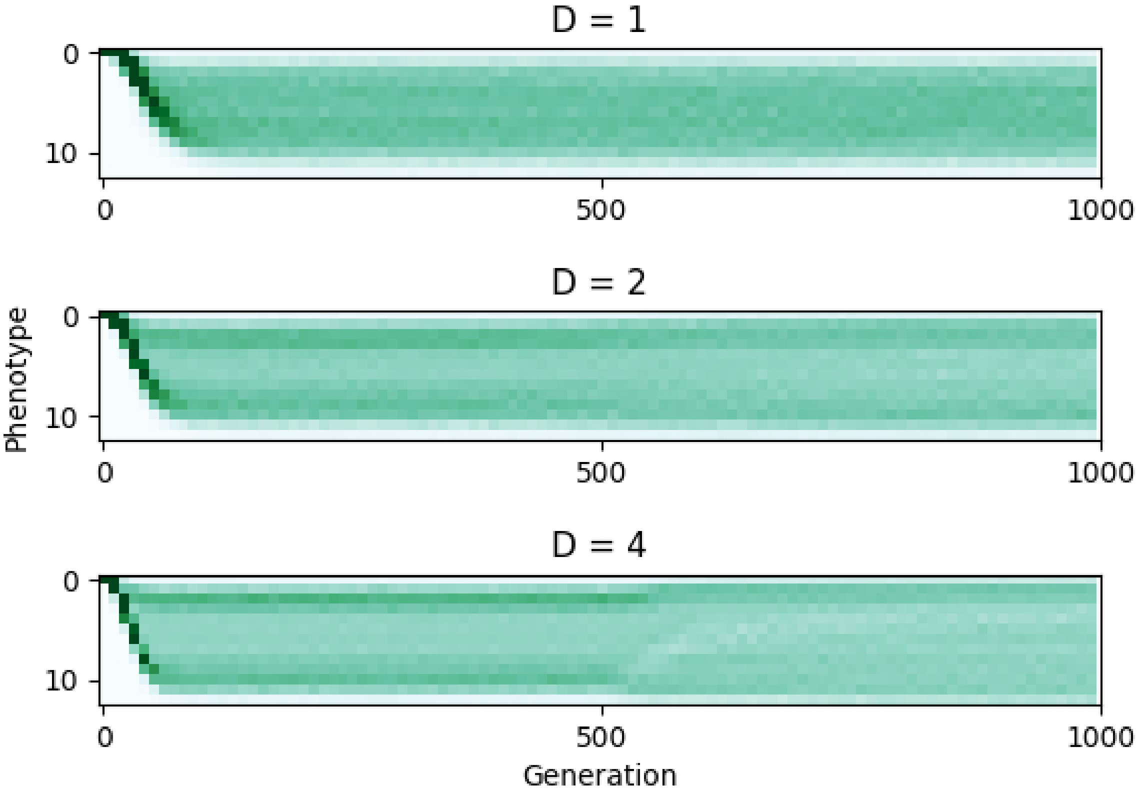

Fig. 4: Temporal pattern of phenotype distribution in the community Distribution of phenotypes for every 10 generations is shown. Higher frequency is represented by darker colouration.

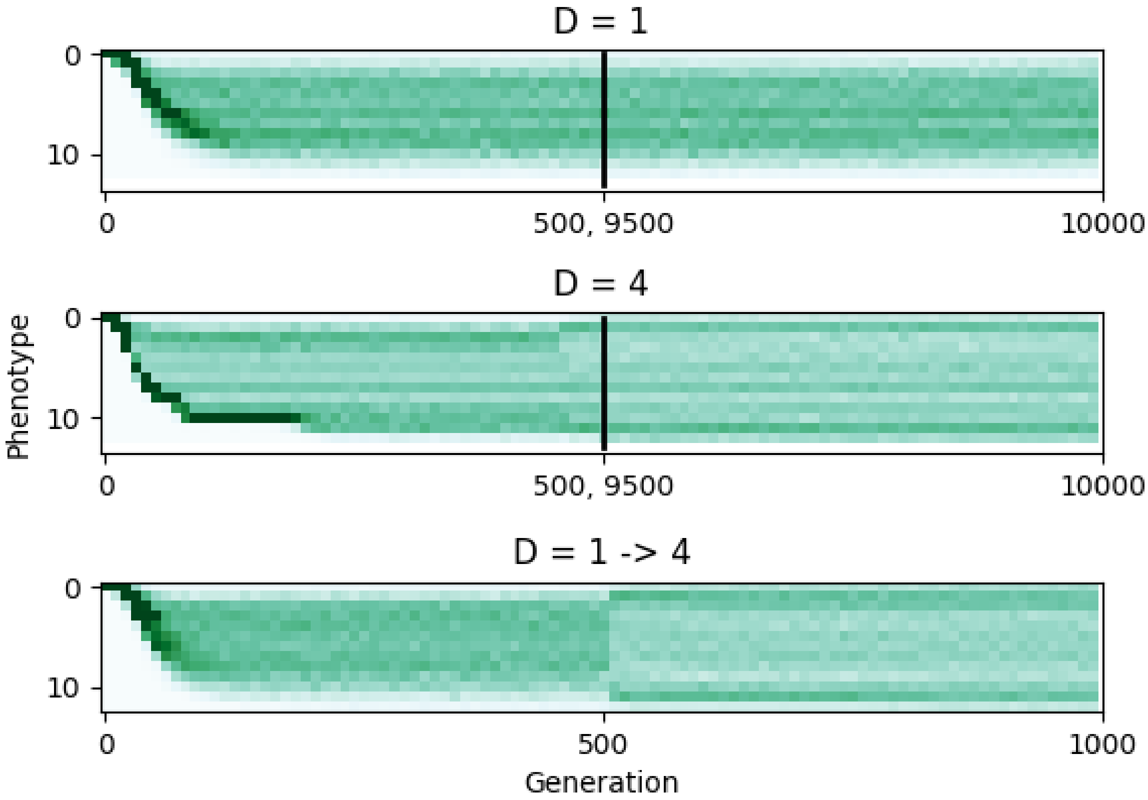

Fig. 5: Temporal pattern of phenotype distribution during 10000 generation for $D = 1$ (uppermost) and $D = 4$ (middle). The results during the period of 500-9500 generations are omitted. The pattern sifted different equilibrium state when D changed from 1 to 4 at the 500 generations (Lowermost). In these simulation, values of parameters used are same as those of Fig. 1 except for $M = 1024$

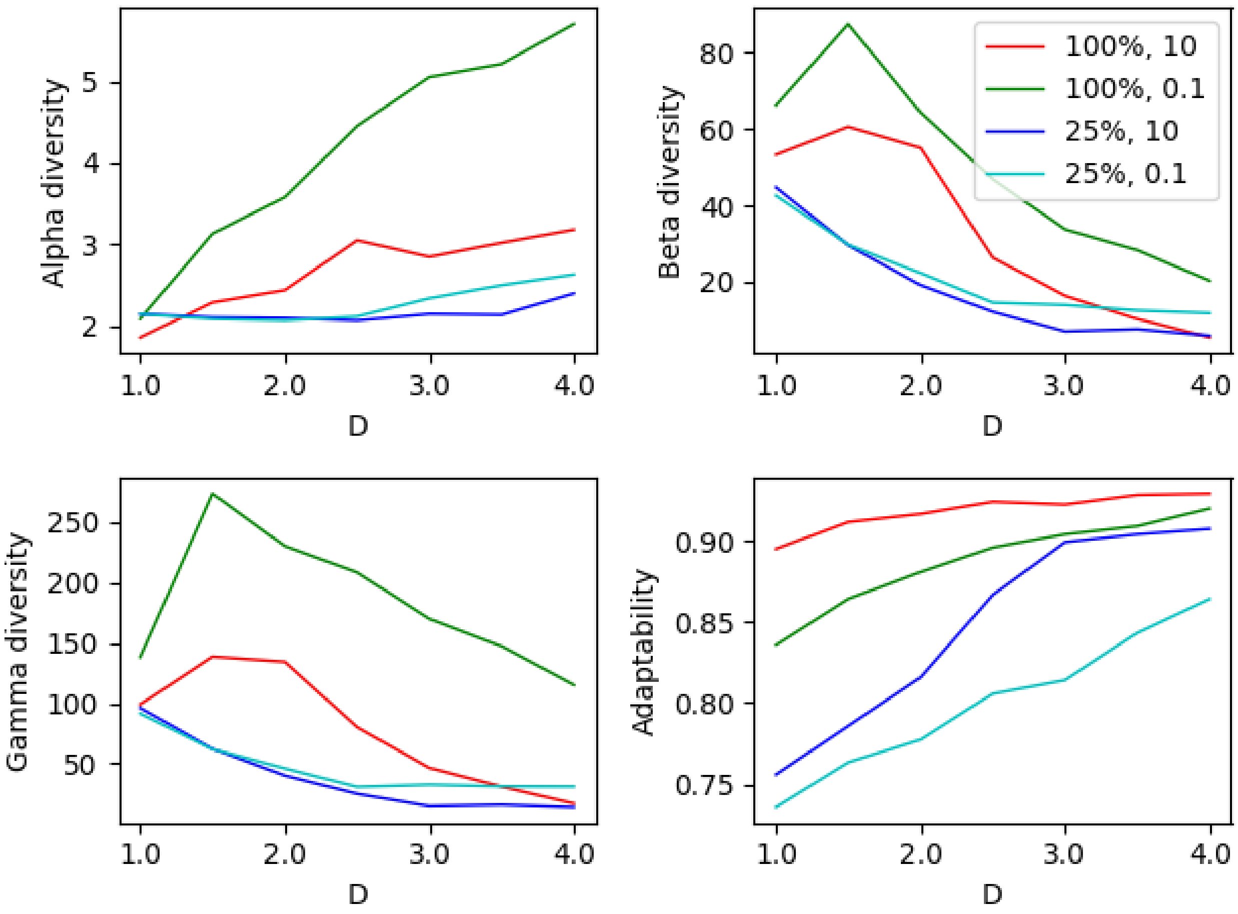

Fig. 6: Results of relationship among dispersal rate (D), population density (d), and species diversity. Under ecological speciation model. Two different values of strength of phenotype isolation ($p = 0.1, 10$) and population density ($d = 0.25, 1.0$) were used respectively. All other parameters are same as Fig. 1.

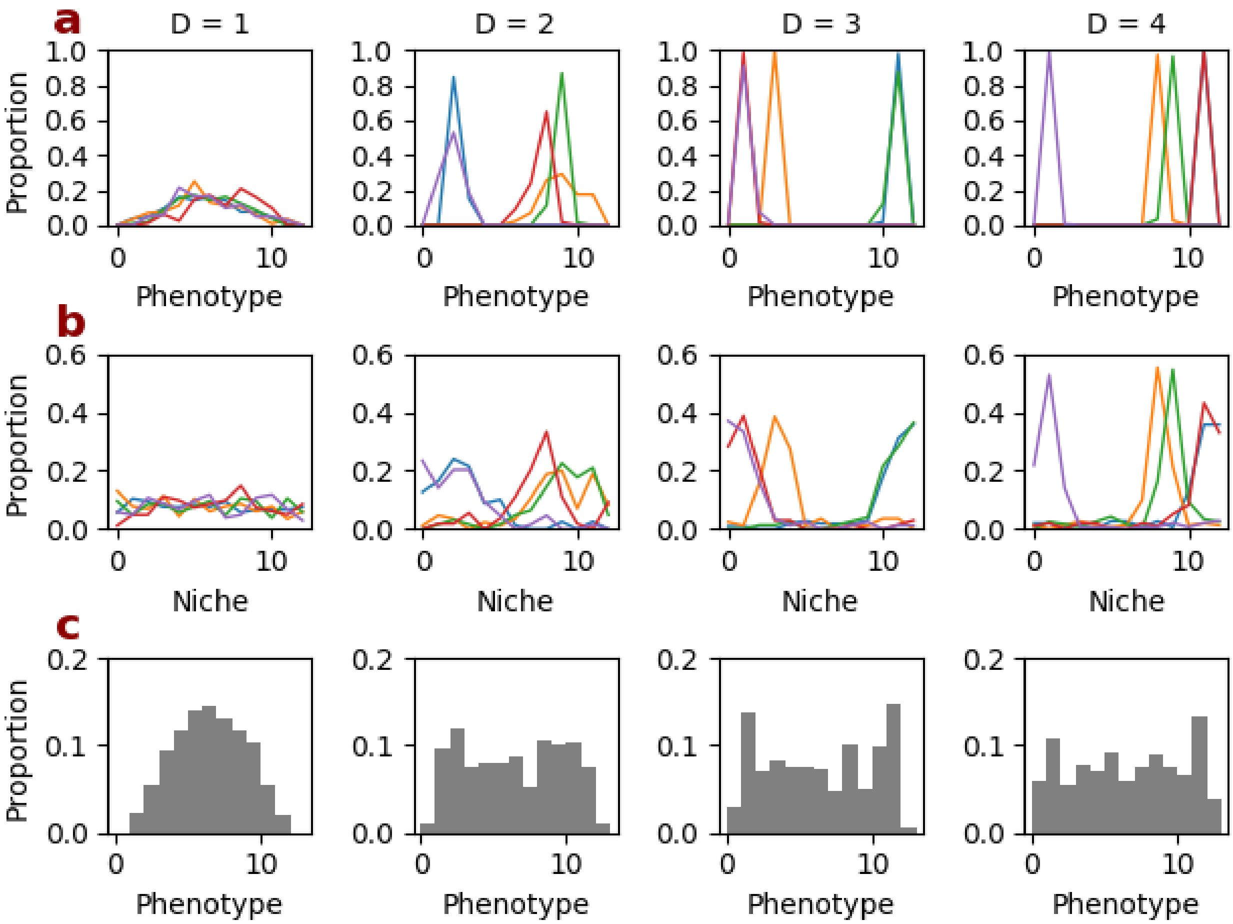

Fig. 7: Frequency distribution of phenotype (a) and niches occupied (b) by each of the five most dominant species at equilibrium under ecological speciation model. Different species are shown in different colours. Frequency distribution of phenotypes in total species is also shown (c). Patterns under different dispersal rates (D) are shown. Population density $d = 1.0$ and strength of reproductive isolation $p = 0.1$

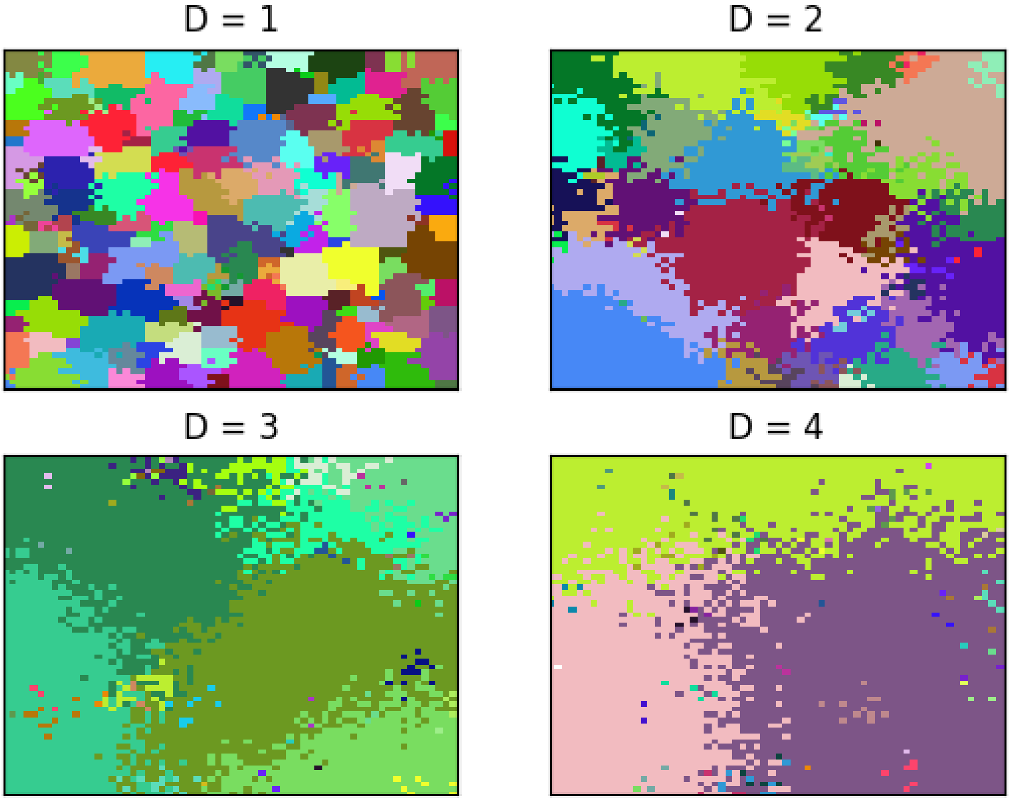

Fig. 8: Geographical patterns of the distribution of species under neutral model. Individuals of different species are shown in different colours. Patterns under different dispersal rates (D) are shown. All parameters are same as Fig. 1 except for mutation rate $\mu = 0.001$.

Although this model did not assume specific physical barriers to gene flow, including mountain ridges and valleys, genetic differentiation by geographical isolation occurred as a result of isolation by distance. We observed the results of the simulation when speciation was assumed to occur only by genetic drift and isolation by distance. The community exhibited a rapid increase of species followed by decreasing speciation rates and finally attained a steady state with a very low speciation and extinction rate. At equilibrium, the frequency distribution of phenotype values for each species showed a bell-shaped curve with a single peak at the particular phenotype value (Fig. 1).

First, we observed the results when population density was high ($N > M/2$). Numbers of identifiable phenotypes decreased with decreasing dispersal rate (D). The phenotypes of almost all species were similar because of convergent evolution when the dispersal rate was very low ($D = 1$) (Fig. 1). In this case, various habitats were equally occupied by species with similar phenotypes, and no difference was noted in habitat use among different species. The distribution pattern of phenotypes did not correspond to that under neutral process (Fig. 8), indicating that convergent selection is a dominant process. In contrast, more than four distinctive phenotypes appeared when the dispersal rate was high ($D = 4$), and 2 or 3 distinctive phenotypes appeared under a moderately high dispersal rate ($D = 3$) (Fig. 1). Based on the frequency distribution curve, each habitat was occupied by the species with a particular phenotype that was most adapted to its habitat. In this model, stable co-existence of different ecotypes was not observed within the same species. Thus, when the dispersal rate was high, each phenotype represented an ecotype.

Patterns of spatial distribution for each species radically differed with change of dispersal rate (Figs. 2 and 3). When the dispersal rate was low, individuals of the same species became spatially aggregated and different species distributed parapatrically and allopatrically, revealing geographical patterns resembling a chequerboard. Thus, when the dispersal rate was low, species of the same phenotype appeared parapatrically and allopatrically, representing patterns of non-adaptive radiation. In contrast, when the dispersal rate was high, geographical positions of individuals of different species were spatially mixed. Individuals co-existed within a local area, and several species of diverse ecotypes occupied different habitats, which represents adaptive radiation.

The community structure shifted to a different state if dispersal rate changed, regardless of its initial condition. For example, the equilibrium community including diverse ecotypes (an outcome of adaptive radiation) shifted to a state of non-adaptive radiation when dispersal rate decreased (Fig. 4). After the community reached equilibrium, the pattern of ecotype composition and species distribution was stable over time (Fig. 5).

Next, we observed the results when population density was low ($N < M/2$). Divergence of phenotypes and habitat use (i.e. ecotypes) occurred when the dispersal rate was very high ($D = 4$). However, decrease in dispersal rate yielded a community in which species with the same phenotype were distributed parapatrically, and no divergence of habitat use occurred among these species.

Species richness differed depending on population density. In a community with a high population density ($N > M/2$), local species richness monotonically increased with increase in dispersal rate, whereas total species richness was the maximum at an intermediate dispersal rate (Fig. 3). Level of specialisation in habitat use and diversity of phenotypes increased with an increase in dispersal rate. Decrease in population density decrease in the level of specialisation in habitat use.

The same results as detailed above were obtained when ecological speciation was allowed to occur. Changing the tightness of the linkage between ecological traits and reproductive traits did not change the relationship between dispersal rate and patterns of radiation, although it affected the relationship with species richness (Fig. 6, Fig. 7).

3.4 Discussion

Whether speciation occurs by genetic drift and isolation by distance or by ecological speciation, both adaptive and non-adaptive radiation can occur, and it does not largely affect the patterns of radiation. Based on our model, the most extensive adaptive radiation occurs in lineages with high population density and relatively high dispersal rate. The typical pattern of radiation, which is rapid species diversification followed by decrease in speciation and extinction rate, can be detected even in the model assuming only neutral processes of speciation and community dynamics, because this pattern reflects community dynamics rather than speciation processes. So, this temporal pattern is not restricted to a particular model of speciation. The previous model, assuming only neutral processes, shows that speciation rate is more accelerated in the populations with higher density, implying that radiation is characteristic of lineages with high population density.

Competitive interaction is the major cause of differences between adaptive and non-adaptive radiation. When dispersal rate is high, species formed by geographical isolation expand their habitat range and mix with other species. Because of frequent interaction among different species, interspecific competition becomes more intense than intraspecific competition, resulting in divergence in phenotypes among species by character displacement. In contrast, when the dispersal rate is low, aggregation of species occurs and sharp boundaries are created among the distributions of different species. In this case, interaction among different species is limited to the individuals on these boundaries, and therefore, intraspecific competition is more intense than interspecific competition, which results in the convergent evolution of phenotypes. Different species cannot coexist within a local area because of competition among ecologically equivalent species. In addition, the effects of reproductive interferences become more pronounced as dispersal ability decreases because of decrease in area in which individuals can find mating partners. This may contribute to preventing individuals of different species staying in neighbouring patches.

These findings explain why patterns of both adaptive and non-adaptive radiation are found in organisms on oceanic islands. Because of fewer predators, lineages on oceanic islands tend to have a higher population density than those on continents. Thus, depauperate environments are most likely to constitute patterns of non-adaptive radiation as well as adaptive radiation, although further studies are required to compare how patterns of diversification differ between oceanic islands and continents.

In this study, the direction and distance of dispersal of individuals is assumed to be random. Results may differ given individual choice in moving to new habitats. Although we did not factor in this assumption for the sake of simplicity of the model, the essential aspects of the results should be the same in both the cases. Individuals with very low dispersal ability cannot reach preferable habitats despite choice, but those with high dispersal ability can reach the habitats that they choose. Therefore, ability to choose preferable habitat is related to dispersal ability. Most examples of non-adaptive radiation are found in organisms with low dispersal ability such as land snails, salamanders and damselflies (Gittenberger, 1991; Holland & Hadfield, 2004; Cameron, Cook & Hallows, 1996; Wake, 2006). In contrast, high dispersal ability lineages, e.g. birds, exhibit few examples (Uy, Moyle & Filardi, 2009) of non-adaptive radiation and an abundance of examples of adaptive radiation (Schluter, 2000). This supports our results in that both original and apparent non-adaptive radiation is most likely to occur in lineages with low dispersal ability. Allopatric and parapatric distributions of species without ecological and morphological differences are often regarded as premature stages of progress in diversification. However, these results show that this is not necessarily the case. The saturated community with high species and ecological diversity (i.e. equilibrium state of adaptive radiation) can shift to a community comprising parapatric and allopatric species of single ecotype (i.e. equilibrium state of non-adaptive radiation) by decrease in dispersal rates of the lineages. This means that non-adaptive radiation is not a preliminary step in adaptive radiation. Various factors affect dispersal ability, e.g. life history, habitat use and climate, and therefore, the community may adapt to either of these states. Except in cases of an extremely high dispersal rate, numbers of ecotypes increase with increasing dispersal rate, and thus, only a few ecotypes with a fairly low dispersal rate emerge in the community. This situation appears to correspond to parallel radiation or replicated adaptive radiation, in which only a few ecotypes evolve independently in different lineages.

Differences between adaptive and non-adaptive radiation arise only as a consequence of changes in dispersal rate and population density, and reflect differences in the dominant mode of selection, i.e. convergent or divergent selection, operating in the community. Thus, the pattern that has been called non-adaptive radiation is, in fact, promoted by the adaptive process as well as adaptive radiation. Their difference has no relationship with the difference between natural selection and genetic drift that has been a focus of controversy over 100 years.

3.5 Table

Table 1: Parameters used in the model and their values

Symbol	Value	Description
G	1000	Number of generation
q	64	Length (number of patches) of each side of the space
M	4096	Number of patches
d	0.25 to 1.00	Population density
N	1024 to 4096	Number of individuals
l_r	512	Length of genes controlling reproduction
h	16	Threshold value for reproductive isolation
l_p	12	Length of genes controlling phenotypes
K	12	Maximum number of niches
D	1.0 to 4.0	Dispersal rate
m	0.2	Migration rate
μ	0.0002	Mutation rate
p	0.1 or 10	Strength of reproductive isolation (used in the ecological speciation model)
H	0 to 12	Phenotype value

4 The relationship of habitat diversity and spices richness

4.1 Introduction

A high level of species diversity is a crucial element that increases ecological functions and maintains stable condition of ecosystems (Isbell et al. 2009). Diversity of habitat has been thought as a major element that enables coexistence of many species and evolution of high species diversity (MacArthur & Wilson, 1967; Davidowitz &Rosenzweig, 1998). Presence of diverse habitat promotes ecological speciation due to segregation of habitat use and ecological character displacement, yielding high species diversity in the community (Schluter 2000; Grant & Grant 2006; Nosil 2012). There are many examples of species diversification in association with habitat diversity, such as endemic organisms on oceanic islands and isolated lakes, where species adapted to particular niches and diversified, yielding adaptive radiation (Grant 1999, Schluter 2000; Parent & Crespi 2009). In addition, environments with presence of various habitats can minimize competition among species and increase numbers of coexisting species, if species inhabit complementary niches with some alternative resources (Brockhurst et al. 2006; Ashton et al. 2010). Conversely, habitat loss and decrease of habitat diversity are the most serious threats for biological diversity (Fahrig 2003; Ewers & Didham, 2006). These suggest that species diversity increases with increase of habitat diversity (Reynolds et al. 1997; Chesson 2000; Stein & Kreft 2014).

However, some recent studies have suggested that high level of species diversity is not necessary associated with levels of heterogeneity of environments and presence of diversity of available habitats (Gazol et al. 2013; Laanisto et al. 2013). In addition, there are some empirical studies that show existence of extremely high species diversity in soil organisms on fairly uniform environments such as limestone outcrops (Schilthuizen et al. 2001, Schilthuizen & Rutjes 2004; Wada & Chiba 2013). These examples show that species diversity may become to reach a high level regardless of levels of heterogeneity of environments and diversity of available niches. Absence of relationship between species diversity and habitat diversity may be explained by the ecological neutral theory, which considers only stochastic process without niches and interspecific competition (Hubbell 2001). Under this model, species diversity is mainly determined by community size and immigration rates. However, it is unlikely that ecologically neutral relationships among different species can persist in heterogeneous environments. Local adaptation should occur in heterogeneous environments at long evolutionary time scale, which break the neutrality.

In the present study, I focus on niche conservatisms as factors that alter the relationship between diversity of available habitats and species richness. Niche conservatism is the tendency of species to limit evolutionary change and retain ancestral ecological characteristics (Wiens & Graham 2005; Wiens et al. 2010). Fundamental niche can be conserved over long evolutionary timescales due to physical limit for adaptive change (Peterson et al. 1999; Wiens & Graham 2005), which is an outcome of adaptation to particular habitat. This sort of evolutionary constraints may prevent habitat shift. If so, how do niche conservatisms alter the relationship between habitat heterogeneity and species diversity? Niche conservatisms are likely to be more effective in the environments composed of discontinuous habitats than those of continuous habitats, because evolutionary niche shift is difficult to occur in discontinuous habitats. In addition, effects of niche conservatisms on species diversity may be more serious in the organisms with low dispersal ability.

I hypothesize that a positive correlation between habitat diversity and species diversity evolves in the landscape with continuous habitats, but not in the landscape with discontinuous habitats. In addition, I hypothesize that low dispersal rates intensify the effects of local adaptation and niche conservatisms on this difference. I test these hypotheses by using individual-based model constructed in the previous sections.

4.2 Methods

We constructed individual-based stochastic patch model expanding the model of chapter.2. Individual is defined as diploid and hermaphroditic. An individual has two sets of genes that relate to incompatibilities in reproduction and to phenotypic values, respectively. Each time unit is assumed to comprise experience four steps: reproduction, dispersal, mutation, and speciation.

The hypothetical island is represented by a two-dimensional square lattice with an M number of grid cells, each of which denotes a habitat patch. Difference in the habitat condition is represented by the parameter from 0 to K (Fig. 1). The condition of the habitat is invariant during the single simulation. I used two types of assumptions in terms of landscape structure. First, in the continuous habitat model, I assumed that the landscape is composed of continuous habitats. Each habitat condition is represented numerically by integer number from 0 to K, and these numbers were assigned for each habitat patch. Second, in the discontinuous habitat model, I assumed that the landscape is composed of discrete habitats. Discrete numbers were assigned for each habitat patch. The value of K (habitat diversity) changed from 0 to 12.

Dispersal rate of the individuals D changed from 1 to 4. Average species richness was calculated at the equilibrium condition of each simulation run during 901-1000 generations. Details of other parts of the model are same as those described in chapter.3.

4.3 Results

The relationship among habitat diversity, species richness and dispersal rates observed was consistent among different simulation runs. Changes in total numbers of patches did not affect the relationships. In addition, the overall characteristics of the relationship were not affected by the changes in mutation rates. Species richness reached equilibrium after 900 generations, and showed no clear decline or increase thereafter.

In the continuous habitat model, a positive correlation was found between habitat diversity (K) and species richness, and species richness represented the highest value when the environment had the highest habitat diversity (Fig. 2). Although this relationship is invariant, dispersal rate changed species richness. Increase of dispersal rate (D) resulted in decrease of species richness (Fig. 2).

In the discontinuous habitat model, species richness showed a humped shape relationship with habitat diversity (Fig. 3). Although this relationship was invariant in terms of dispersal rates, the habitat diversity showing the highest species richness changed with the change of dispersal rate. Species richness became higher in the environments with low habitat diversity when dispersal rate was low ($D = 1$) (Fig. 3). In addition, the highest species richness was observed when $D = 2$, indicating that species richness became highest under intermediate dispersal rates.

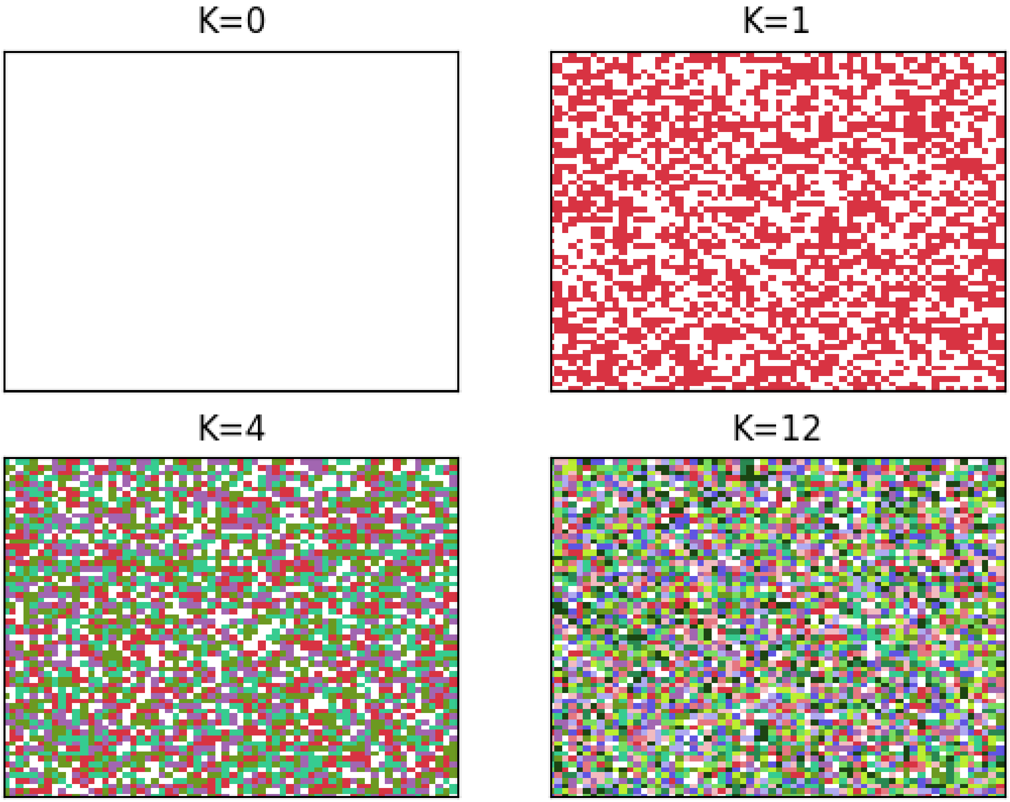

Fig. 1: The examples of distribution of different habitats on the 64×64 field. Different habitats are shown in different color. The condition of the habitats was randomly assigned at the beginning of the simulation.

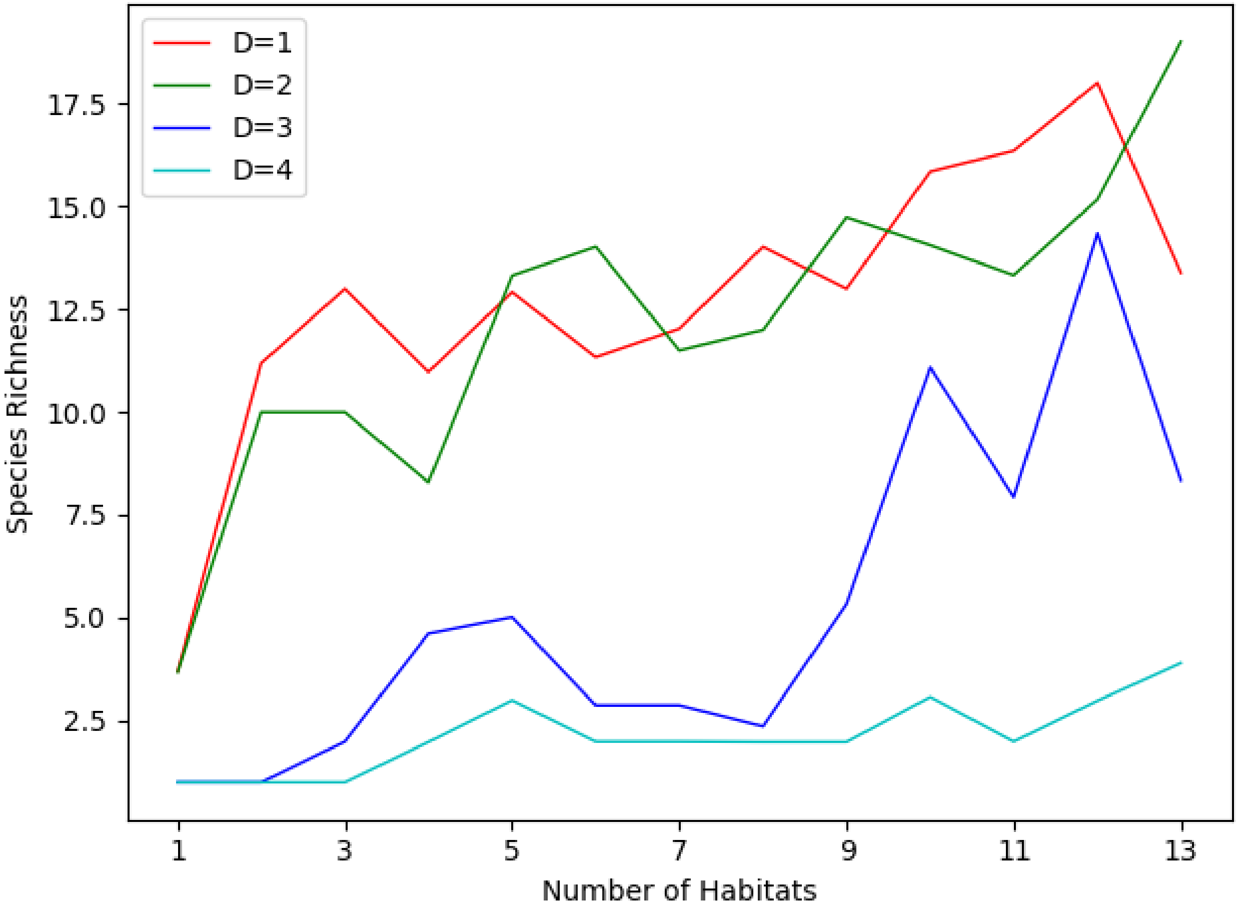

Fig. 2: The equilibrium species richness in continues habitat model. Field size is 32 × 32. All other parameters were same as those in Chapter 3.

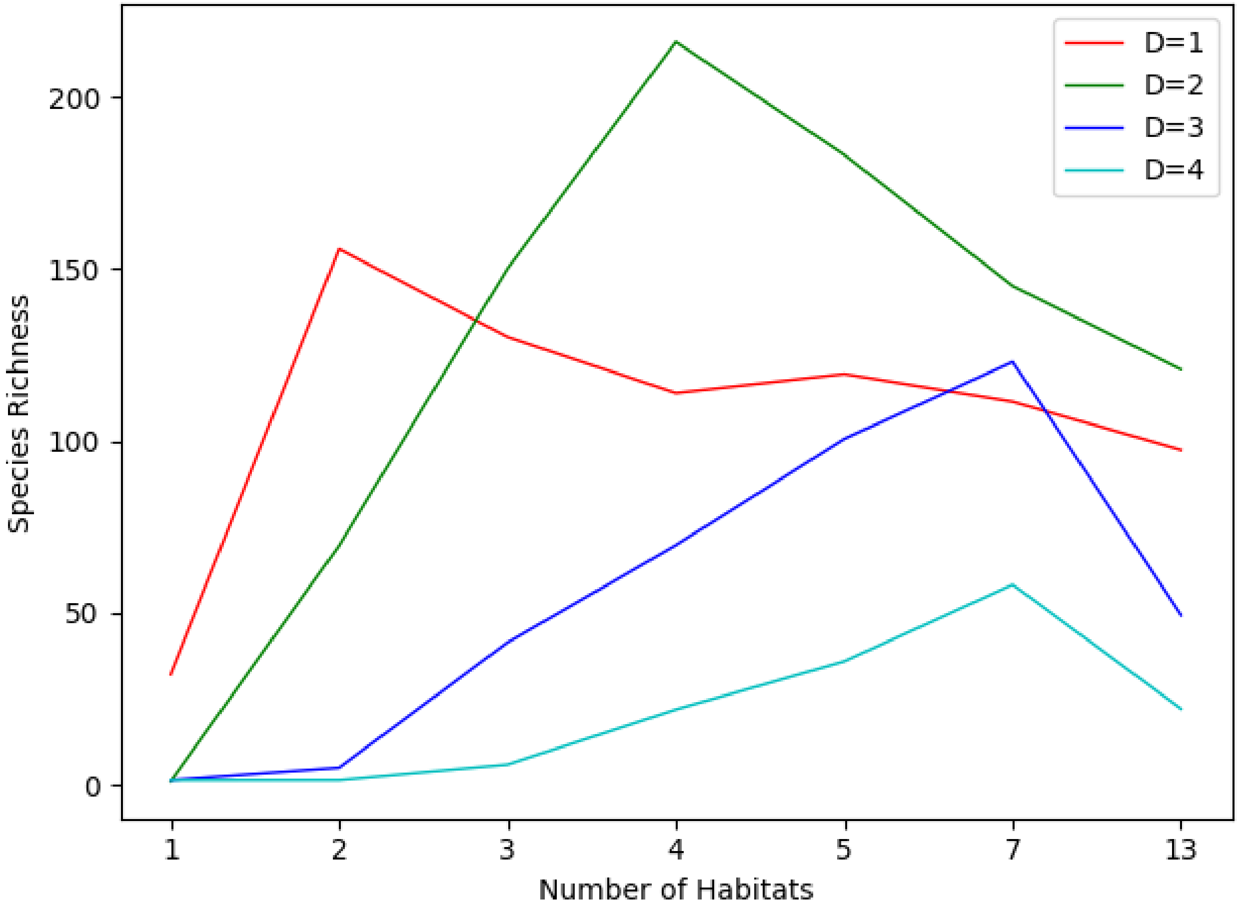

Fig. 3: The equilibrium species richness in discontinues habitat model. Field size is 32 × 32 and their density is 1.00(100%). All other parameters were same as those in Chapter 3.

4.4 Discussion

The ‘habitat heterogeneity hypothesis’ assumes that structurally complex habitats provide more niches and more diverse ways to utilize resources (MacArthur & Wilson, 1967; Bazzaz, 1975; Davidowitz & Rosenzweig 1998; Stein & Kreft 2014), which increase species diversity. Heterogeneity includes both diversity of habitat types and distinctiveness of each habitat type. The present results show that both of these elements of heterogeneity strongly affect species diversity. Whether condition of habitats is continuous or discontinuous affect species diversity as well as number of different types of habitats.

The relationship between habitat diversity and species diversity differs depending on the continuity of habitats. This result supports my hypothesis that a positive correlation between habitat diversity and species diversity evolves in the landscape with continuous habitats, but not in the landscape with discontinuous habitats. When the landscape is composed of discontinuous habitats, adaptation of populations to particular habitats promotes ecological speciation, resulting in evolution of species occupying limited habitat types. Because of niche conservatisms, niche shift is difficult to occur among such discontinuous habitats. This means that increase of habitat diversity enhances species diversity. Low dispersal rates enhance local adaptation and speciation, increasing species richness. However, in the environment with overly diverse habitats, the species specialized to a particular habitat cannot persist during a long time because of scarcity of the same habitat. Therefore, species richness rather decreases in the environments with the highest habitat diversity. Low dispersal rates promote local extinction of the species specialized to particular habitat, causing further decrease of species richness in the environment with high habitat diversity. Thus, a humped shaped pattern arises in the relationship between habitat diversity and species diversity in the environment with discrete habitats.

When landscape is composed of continuous habitats, species can easily shift their habitat use from one type to the others because of relatively low niche conservatisms. Thus, species can stably persist for long term in the environments with the highest habitat diversity, and a positive correlation arises in the relationship between habitat diversity and species diversity. These support the hypothesis that niche conservatisms affect this relationship particularly when dispersal rate is low.

The present study suggests that evolution of organisms on the landscape with continuously differentiated habitats yields a positive correlation between species richness and habitat diversity. In contrast, this positive correlation is restricted in the environment with low habitat diversity when the landscape is composed of discontinuous mutually discrete habitats. In this case, a rather negative correlation arises in the environment with high habitat diversity. As a result, all of the positive, negative and non-significant correlation can be observed in the relationships between habitat diversity and species diversity.

Although a positive correlation between habitat diversity and species diversity has been widely documented in various organisms (Stevens & Carson 2002; Questad & Foster 2008; Stein & Kreft 2014; Stein et al. 2014), several other studies have recently documented negative, unimodal or non-significant correlations (Lundholm 2009; Tamme et al. 2010; Gazol et al. 2013; Laanisto et al. 2013). Findings of these empirical studies are consistent with the present results. Further studies are needed to compare the present results with the results obtained in nature, because the assumption of the present model is overly simplified. However, these findings suggest that continuity of different habitat elements is crucial in understanding the role of habitat diversity on species diversity.

5 General discussion

This study raises three new viewpoints in terms of processes arising species diversity patterns. First, neutral theory had become possible to apply to problem that could not be handled so far by expanding it. Chapter 2 showed that the pattern of speciation burst typically observed in organisms in depauperate environments could occur under conditions of neutrality. The accelerated speciation in the initial stage of radiation and the subsequent decline in speciation can be explained without assuming the existence of vacant niches and interspecific competition.

Second, adaptive and non-adaptive radiation are not different concepts, both ends of one continuous phenomenon (Chapter 3). Most examples of non-adaptive radiation are found in organisms with low dispersal ability such as land snails, salamanders and damselflies (Gittenberger, 1991; Holland & Hadfield, 2004; Cameron, Cook & Hallows, 1996; Wake, 2006). In contrast, high dispersal ability lineages, e.g. birds, exhibit few examples (Uy, Moyle & Filardi, 2009) of non-adaptive radiation and an abundance of examples of adaptive radiation (Schluter, 2000). This supports our results in that both original and apparent non-adaptive radiation is most likely to occur in lineages with low dispersal ability.

Finally, greater habitats diversity does not necessarily bring greater species richness (Chapter 4). The present study suggests that evolution of organisms on the landscape with continuously differentiated habitats yields a positive correlation between species richness and habitat diversity. In contrast, this positive correlation is restricted in the environment with low habitat diversity when the landscape is composed of discontinuous mutually discrete habitats. In this case, a rather negative correlation arises in the environment with high habitat diversity. As a result, all of the positive, negative and non-significant correlation can be observed in the relationships between habitat diversity and species diversity.

These conclusions obtained from three separate studies yield one simple conclusion: the observed diversity patterns look like exclusive from each other do not necessary imply underlying independent processes. A same process may create distinctive spatial and temporal patterns of species diversity depending on the difference in structure of landscape and population structure. In general, spatial and temporal diversity patterns in nature are difficult to regulate to test of the hypothesis using experiments. Particularly, dynamics of long-term diversity patterns are difficult to reproduce except for experiments with microcosms. Individual based simulation is a powerful tool to address these issues. However, empirical evidences are still required to test the ideas raised in the present study. Future studies using experiments with microcosms, macroecological surveys and paleontological studies using large amount of database would be required. In addition, further information of genetic background of species is required to incorporate the present model with these empirical data. Integrated analyses among database of global species diversity patterns, genetic information, and theoretical models are crucial in future studies.

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