

Invasion of vacant niches and subsequent sympatric speciation

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An individual-based simulation study was conducted to examine the population dynamics of ‘invasion of a vacant niche’ and subsequent speciation (by reproductive isolation) when food resources are randomly distributed spatially within the habitat and the frequencies of different food types are bimodally distributed (i.e. smaller and larger sizes of food being most abundant). The initially vacant niche was that of unused larger sizes of food. When phenotypic variation for resource use (i.e. food sizes) was small in the initial population, and each female could choose a mate from anywhere in the habitat, the population could not invade the vacant niche. But when the dispersal distance of the offspring and the area within which a female could choose a mate were small (i.e. the genetic neighbourhood size was small), the population could, in most cases, evolve to use both smaller and larger food sizes and form sister species sympatrically, with each species utilizing one of the two niches (small and large sizes of food). When phenotypic variation in resource use in the initial population was large, the population could, in most cases, invade the vacant niche by evolving to use both smaller and larger sizes of food. The probability of speciation increased as the dispersal distance of offspring decreased. The results indicate that populations whose individuals have small Wright’s genetic neighbourhoods may often exploit a vacant niche and diversify sympatrically in the process.

Keywords: ecological divergence; reproductive isolation; sympatric speciation; vacant niche

1. INTRODUCTION

Lineages have often been considered to diversify most rapidly when ‘vacant niches’ are not occupied by other species (Mayr 1942; Simpson 1944). In the Hawaiian archipelago, for instance, insects such as crickets and *Drosophila* flies diverge to many species occupying diverse niches that, in other regions, are held by taxonomically disparate organisms (Wagner & Funk 1995; Futuyama 1998). Fossil records also indicate that the radiation of one group of organisms follows the extinction of other groups, as when mass extinction took place (Rosenzweig & McCord 1991; Benton 1996; Seploski 1996). In addition, recent studies show that invasion of novel habitats plays an important role in adaptive divergence and speciation (Orr & Smith 1998; Schluter 1998).

If such diversification by speciation is sympatric, then it involves two distinct processes (Johnson & Gullberg 1998). First, in the process of the ancestral population evolving, a subdivision is created whose individuals utilize the vacant niche. Second, this subdivision becomes reproductively isolated from the ancestral population, which continues to use the original resources. This poses the following problem for sympatric speciation by means of invasion of a vacant niche.

Suppose that food size is distributed bimodally (smaller size and larger size), and that in the past the ancestral population has used only smaller sizes of food. If intermediate sizes of food happen to be relatively abundant, a segment of the ancestral population can evolve from using smaller sizes of food to using larger sizes, through first evolving to use the intermediate sizes. However, if individuals using smaller sizes of food can easily interbreed with those using larger sizes, and their offspring, using intermediate sizes of food, can survive and reproduce, as is

expected to be the case for the beginning phase of invading a second niche, then the opposition of recombination to formation of distinct subdivisions of the population, and evolution of reproductive isolation between the subdivisions, can be insurmountable. In other words, the problem lies in the second process of sympatric speciation, that of reproductive isolation of subpopulations.

At the same time, at the other end of the spectrum, if intermediate sizes of food are rare or absent, the first process of speciation can be difficult to achieve: that of the ancestral population invading the unexploited niche of larger sizes of food. A single qualitative mutational leap is then required, as a sequence of small quantitative mutational steps will not work. Thus, given these conflicting requirements of sympatric speciation for the extremes in relative abundance of intermediate food sizes when food size is bimodally distributed, circumstances that allow sympatric speciation via the invasion of a vacant niche may be very particular from a theoretical point of view.

The occurrence of sympatric speciation, in any manner, has been considered to present some theoretical difficulties (Mayr 1942; Maynard Smith 1966; Felsenstein 1981; Rice & Hostert 1993; Futuyama 1998; Kondrashov *et al.* 1998), with the main problem being recombination, which destroys association between alleles for adaptation and alleles for assortative mating (Felsenstein 1981; Rice & Hostert 1993), unless it is somehow avoided or prevented. However, a number of studies provide empirical evidence for sympatric speciation (Bush 1994; Orr & Smith 1998), and new models that explain sympatric speciation have recently been proposed (Turner & Burrows 1995; Doebeli 1996; Johnson *et al.* 1996; Payne & Krakauer 1997; Kondrashov & Shpak 1998; Dieckmann & Doebeli 1999; Higashi *et al.* 1999; Kondrashov & Kondrashov 1999).

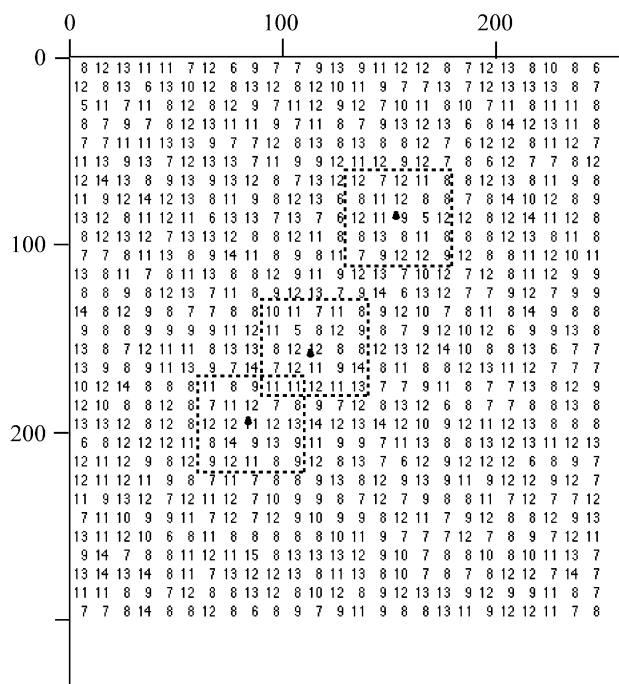


Figure 1. An example of spatial resource distribution in a simulation habitat. Only a 300 × 300 area of the 700 × 700 area is shown. Small values indicate the values for food types within the 10 × 10 cells. Black circles are examples of the location of individuals searching for foods within the dashed 25-cell squares (5 × 5).

These models suggest that several different factors can promote sympatric speciation: for example, habitat preference and mating in the same habitat (Johnson *et al.* 1996); disruptive selection and assortative mating (Dieckmann & Doebeli 1999; Kondrashov & Kondrashov 1999); sexual selection (Turner & Burrows 1995); and mating-dependent dispersal (Payne & Krakauer 1997). Many of these models are limited to examining only one of the two processes of sympatric speciation instead of both. In the model described by Kondrashov & Kondrashov (1999), the invasion of a new niche is considered, but disruptive selection for ecological traits (e.g. resource use) is assumed to favour the most extreme phenotypes (Tregenza & Butlin 1999).

In many organisms, the dispersal of offspring is often limited; therefore, the genetic neighbourhood size can be commensurately limited or small. The genetic neighbourhood size was calculated as $N_b = 4\pi\delta\sigma^2$ where δ is the population density and σ^2 is the parent-offspring dispersal variance (Wright 1943, 1946). The genetic structure of the population caused by small genetic neighbourhood size affects ecological and evolutionary processes (e.g. Kawata 1995, 1996), and so, examining the effect of genetic neighbourhood size on speciation processes can be important, or even essential in models that incorporate spatial structure.

This study presents an individual-based model to examine the dynamics of invasion of a vacant niche followed by within-population divergence that can lead toward evolutionary branching and speciation. The model explicitly incorporates spatial structure. A vacant niche exists because a bimodal resource distribution (abundant smaller and larger sizes of food, with less abundant inter-

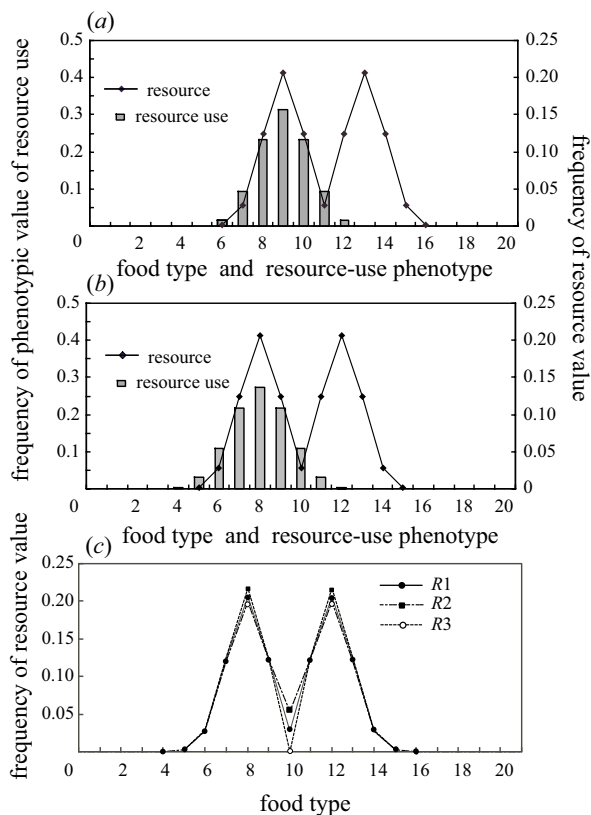


Figure 2. (a,b) Frequency distribution for food-type values and resource-use phenotype values when the initial number of resource-use loci is three (a) and four (b). (c) Three different types of frequency distributions for food types are compared (R1, R2 and R3).

mediate sizes) is assumed, and the ancestral population initially uses only the smaller food sizes. In this model, because food of intermediate size is the least abundant of the three food-size categories, the carrying capacity for individuals using intermediate sizes of food is lower than that for individuals using smaller or larger sizes of food. This complements a major objective of this study: to examine how, under such ecological circumstances, various forms of other conditions (e.g. resource distribution, individual mating tactics, offspring dispersal distance) can promote invasion of a vacant niche, and subsequent within-population divergence leading to speciation, when adaptation and coadaptation includes mutation (instead of only changes in allele frequencies).

2. MATERIAL AND METHODS

(a) *Habitat*

The evolutionary dynamics for a population takes place within a $W \times W$ square (usually $W=700$) area that constitutes the population's habitat. The habitat is subdivided into 10×10 cells, so that when W is 700, there are 4900 cells in the habitat. In this habitat, food resource types (food sizes) are randomly distributed (figure 1) with respect to cells. Eleven food types (types 6–16 or 5–15), based upon a quantifiable property such as size, are assumed to exist; and the frequency distribution for the food types is bimodal (figure 2).

Each cell is occupied by one food type (size), and the probability of a given cell containing a given food type is in

accordance with the frequency distribution for food types. The different food types are randomly distributed with respect to cells (figure 1). For example, if approximately 144 cells are occupied by food type 8, these 144 cells were randomly distributed with respect to the cells in the $W \times W$ space, and therefore, essentially randomly distributed within the habitat, spatially. For simplicity, small-value food types (types 6–11 or 5–10) are called ‘smaller-size foods’, and larger-value food types (types 11–16 or 10–15), ‘larger-size foods’. A population containing individuals using both smaller- and larger-size foods was considered to be a resource-polymorphic population.

(b) Organisms

Each simulated organism has a location (x - y coordinates), sex and reproduces sexually; and each has a set of alleles at loci for female preference (C), female-preference range (explained later) (S), male sexual character (M) and resource use (U). Each of these polygenic quantitative characters is controlled by 10 loci, except for female-preference range. All loci have two alleles (1 and 0), and all are independent from one another. Therefore, in M , C and U , the phenotype value varied from 0 (all loci homozygous for allele 0) to 20 (all homozygous for allele 1). Thus, phenotypic variance is additive and unaffected by environmental variations (i.e. no genotype–environment interaction).

An individual searches for foods within a 50×50 square, which includes 25 cells of the habitat (figure 1). For instance, if an individual is located within the cell located at $x = 80$ – 90 and $y = 190$ – 200 , then it searches for food within the 25-cell region defined by $x = 60$ – 100 and $y = 170$ – 220 . If the individual’s resource-use phenotype is 8, and that food type occupies 4 of the 25 cells, the foraging success (F) of the individual is 4 (i.e. the number of cells in its search area carrying that food type).

However, more realistically, individuals use more than one food type, especially if the types are quantitatively different, and with small differences between close types. Therefore, the case in which an individual uses more than one food type was also considered, and the methods and results are given in electronic Appendix A (available on The Royal Society’s Publications Web site).

Basically, for mating tactics, the threshold-based rule (Gibson & Langen 1996) was applied, whereby females search for their mates until encountering one whose quality exceeds a critical amount. The acceptance range was allowed to evolve. Within a female’s mating area (a circle of radius R), a female with preference value (C) could mate with a male having a male sexual character value (M) if $|M - C| \leq S$ (S = preference range). When no suitable males existed within the mating area, one of three different methods was applied for a given simulation:

- (i) a minimum-distance method, where a female chose the nearest male with a suitable M value;
- (ii) the no-reproduction method, where a female could not reproduce under such a circumstance; and
- (iii) the no-preference model, where a female chose a mate at random within the mating area, independent of male sexual character values.

In addition to the above three methods, another was that of

- (iv) choice for resource phenotype, where the mating procedure is the same as in the minimum-distance model, but females choose mates according to the males’ phenotypes for resource use.

In general, the minimum-distance model was used unless otherwise indicated.

(c) Reproduction and dispersal

After mating, the number of offspring produced by a female depended on the amount of food she obtained, which in turn depended in part on the number of her competitors for food resources. Exploitative competition was assumed, and thus the amount of food obtained by a female was reduced with increasing number of individuals using the same food types as her. The number of offspring produced by a female when each individual used only one food type is calculated as

$$W = \frac{rF}{N} + v,$$

where r is the reproductive rate, F is the foraging success of the individual as mentioned earlier and N is the number of individuals using the same food type within a circle of radius H , which was set at 50, because generally all individuals located within this range could have access to any given food type within the food-search area of the focal individual. The random factor v is a random number obtained from a normal distribution with mean 0 and standard deviation 0.1. As the values of W are real numbers, but the numbers of offspring are integers, the real number W is rounded to the nearest integer. The random factor v was introduced as this avoids having different values of F/N always resulting in the same fitness value because of rounding off. For each of the offspring’s loci, one allele was randomly chosen from the mother, and the other was randomly chosen from her mate. The mutation rate was set at 0.0001 per locus per generation. All parent individuals died after the birth of all offspring.

Offspring dispersed from their birth sites but could not disperse over the entire habitat area. The site to which an offspring dispersed was determined in the following way. The dispersal distance was a random value with a normal distribution having mean 0 and standard deviation d (negative values were converted to positive values). Hereafter, the standard deviation d is called the dispersal distance. The offspring’s dispersal direction was random with a uniform distribution.

(d) Initial conditions

When the initial number of polymorphic loci (among the 10 loci) for characters M , C and U was set at three, the initial frequency of allele 1 was 0.5 for the three polymorphic loci, 1 for three loci and 0 for the remaining four loci; and the frequency distribution of phenotypic values ranged from 6 to 12, as shown in figure 2*a*. When the number of polymorphic loci (among the 10 loci) was set at four, the initial frequency of allele 1 was 0.5 for four loci, 1 for two loci, and 0 for the remaining four loci; and the frequency distribution of phenotypes ranged from 4 to 12 (figure 2*b*). Note that as time proceeds for a simulation, more loci than those that are initially polymorphic can become polymorphic, by mutation. Thus, population evolution in the model includes not only the dynamics of change in allele frequencies, but also the recruitment of loci by mutation.

For each simulation, initially the population used only the smaller sizes of food (figure 2). When 3 of the 10 resource-use loci were initially polymorphic, phenotype values (U) ranged from 6 to 12, and the central intermediate food size was 11. When 4 of the 10 resource-use loci were initially polymorphic, phenotype values ranged from 4 to 12, and the central intermediate food size was 10 (figure 2*a,b*).

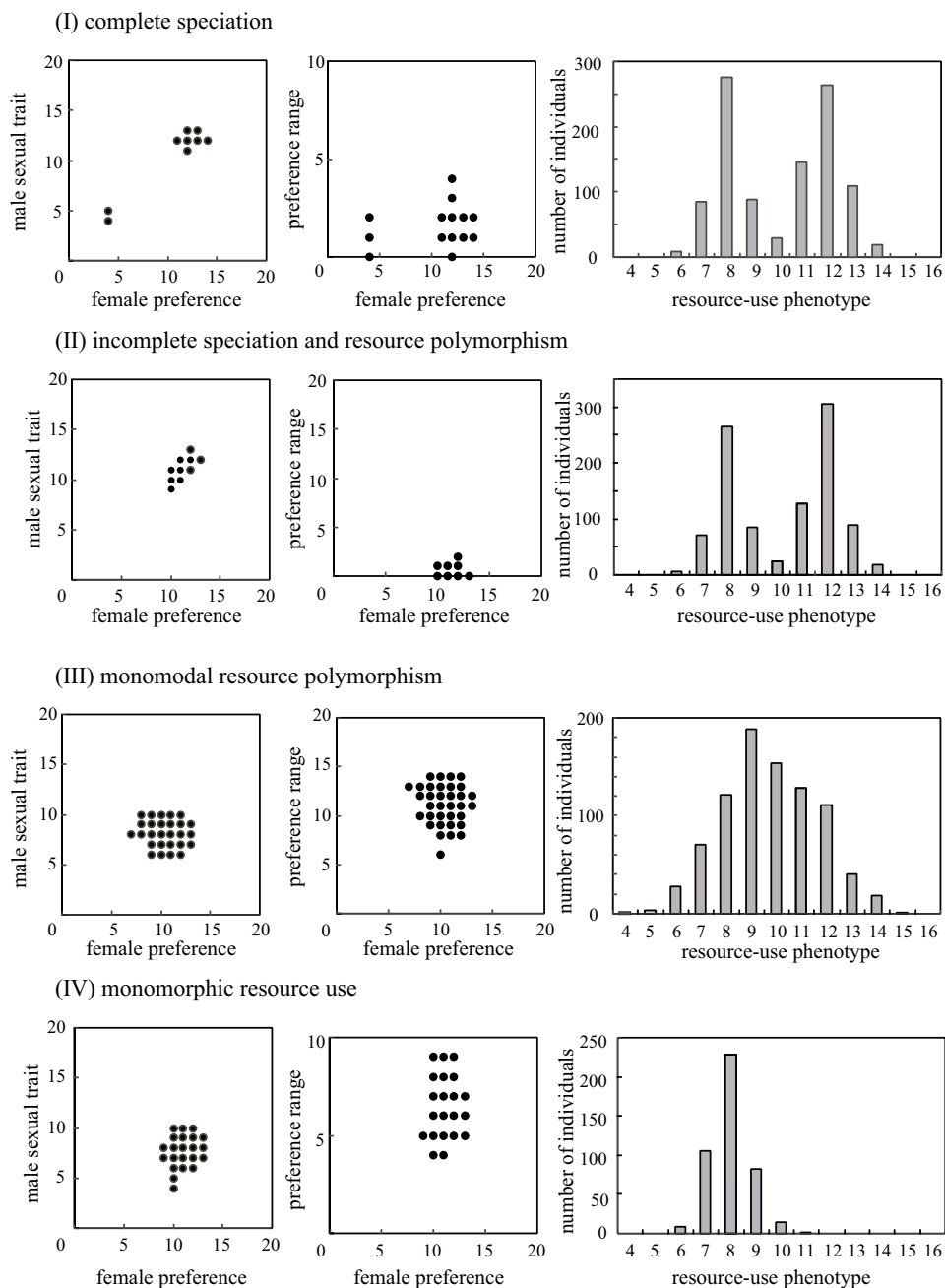


Figure 3. Four categories of outcomes of simulations that ran for 5000 generations. The values of female preference indicate the expressed or unexpressed phenotypic values of female preference (C) for females and males, respectively. The values of male sexual traits indicate the expressed or unexpressed phenotypic values of males or females, respectively. In the case of complete speciation (I) (top row), individuals having female-preference value 4 have a male sexual trait value of either 4 or 5, and the values for female-preference range (S) are 0, 1 and 2. Thus, these individuals do not prefer males having male sexual trait values 11–14. See the text for detailed explanation.

Similar to the resource-use phenotypes, female preference phenotypes (C) and male sexual-character phenotypes (M) initially ranged from 6 to 12 when, initially, there were three polymorphic loci; from 4 to 12 when initially there were four polymorphic loci; or from 2 to 12 when initially there were five polymorphic loci (the initial frequency of allele 1 was 0.5 for five loci, 1 for one locus and 0 for the remaining four loci). With the female-preference range (S), the frequency of allele 1 was set at 0.5 for two loci, and at 0 for the remaining eight loci, so that the phenotype value S ranged from 0 to 4.

Four hundred individuals existed at the beginning of each simulation when $W=700$. When the size of the habitat was

varied, the initial number of individuals also varied, maintaining the same density as in the case of the 700×700 habitat size. For each simulation, the population dynamics within the habitat was examined for 5000 generations, in part by monitoring for each phenotype, every hundredth generation, its frequency distribution of phenotypes within the habitat. In addition, for each simulation, whether the vacant niche had been exploited was determined (i.e. individuals existed that used the larger sizes of food types 12–14); and also whether the subpopulation using the smaller food sizes was reproductively isolated from the subpopulation using the larger food sizes.

Twenty replicate simulations were conducted for each para-

meter setting, and the different parameter settings were obtained by varying dispersal distance (d), mating area (R), number of polymorphic loci, mate searching method and resource distribution. The habitat area size (W) and reproductive rate (r) were also varied and the results are given in electronic Appendix B.

(e) Measurements of spatial structure

To describe the spatial distribution of individuals and phenotypes, Morishita's index of dispersion and semivariance was used. The methods and results are given in electronic Appendix C.

3. RESULTS

(a) Four outcomes of the simulations

For simulations that ran for 5000 generations, there were four categories of outcomes as follows (figure 3).

- (I) Complete speciation occurred, where a subpopulation came into existence that used the unexploited larger food sizes, and then became reproductively isolated from the subpopulation using smaller food sizes.
- (II) Resource polymorphism occurred, where a part of the population used the larger food sizes, but speciation of two subpopulations never occurred. In this case, the female-preference range (C) evolved to small values so that females selectively chose males with regard to male sexual traits. As a consequence, the frequency distribution for resource-use phenotypes was bimodal because of female preference. However, female preference did not become sufficiently strong to eliminate some interbreeding between the part of the population using larger food sizes and that using smaller sizes, so that complete reproductive isolation was not achieved.
- (III) Resource polymorphism occurred, where individuals evolved to use larger food sizes, but resource-use distribution was monomodal, as opposed to category II in which it was bimodal. Also, in contrast to category II, the female-preference range evolved to large values so that mating was essentially random with regard to resource-use phenotypes. Thus, intermediate resource-use phenotypes became the most frequent, even though the availability of food for these phenotypes was small.
- (IV) Finally, monomorphic resource use occurred, where individuals could not evolve to use larger food sizes.

Figure 4 shows the number of individuals for the examples of four categories of simulation outcomes ($d = 50$, $R = 70$, $W = 700$ and $r = 1.6$). For categories I, II and III, there are individuals using the smaller food sizes and individuals using the larger sizes; and therefore, the number of individuals was approximately twice that of category IV.

(b) The effects of initial phenotype variations

From here on, the phrase 'initial number of loci' shall denote the number of those loci controlling a character

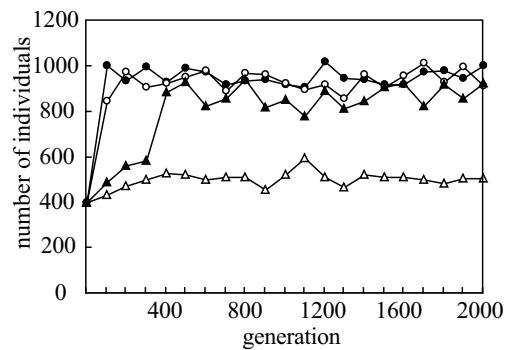


Figure 4. Trajectories of population size for four simulations—each expressing one of the four different types of outcome when female preference follows the minimum-distance model; habitat size is 70×70 cells ($W = 700$); the initial number of loci is three for resource use, male sexual traits and female preference; resource distribution is R1; and $r = 1.6$, $R = 70$ and $d = 50$. In the case of complete speciation (I), reproductive isolation was completed at the 1100th generation of the simulation. Black circles, (I) Complete speciation; white circles, (II) incomplete speciation; black triangles, (III) monomodal resource polymorphism; white triangles, (IV) monomorphic resource use.

that, by virtue of parameter settings for initial conditions, are polymorphic when a simulation begins. When the initial number of loci for resource-use, female preference and male sexual trait was three (figure 2a), all outcomes of the simulations were that of monomorphic resource use (IV), when the mating area for females was the whole habitat ($R = 1000$) and the dispersal distance for offspring were large ($d = 200$). When the genetic neighbourhood size was large (figure 5a), dispersal of genes within the population and habitat was basically uninhibited, which apparently abolished the ability of natural selection to drive sympatric divergence, keeping the genetic content of the population close to that of the initial conditions. On the other hand, when the genetic neighbourhood size was small ($d = 50$ and $R = 70$), so that within-population dispersal of genes was inhibited, all four outcomes could be observed, and the probability of complete speciation was 0.15. The effects on simulation outcomes of different combinations of initial number of loci controlling different characters for $d = 50$ and $R = 70$ are shown in figure 5b. When the initial number of resource-use loci was three, and the initial number of loci for female preference and male sexual traits varied from three to five, the probability of complete speciation (I) was 0.15–0.2. But when the initial number of resource-use loci was four (figure 2b), in all cases, individuals evolved to use larger food resources. The probability of complete speciation (I) increased when the initial number of loci for mating preference and male sexual traits was 4 or larger (0.45).

To illustrate the time required for the process of niche invasion and sympatric speciation, when the initial number of loci for resource-use, female preference and male sexual trait was four, the average number of generations required for complete speciation was 1922 (s.d. = 1249) for $d = 50$, $R = 70$, $W = 700 \times 700$ and $r = 1.6$. The number of generations required for the evolution of resource polymorphism was much smaller than that for reproductive isolation (e.g. figure 4).

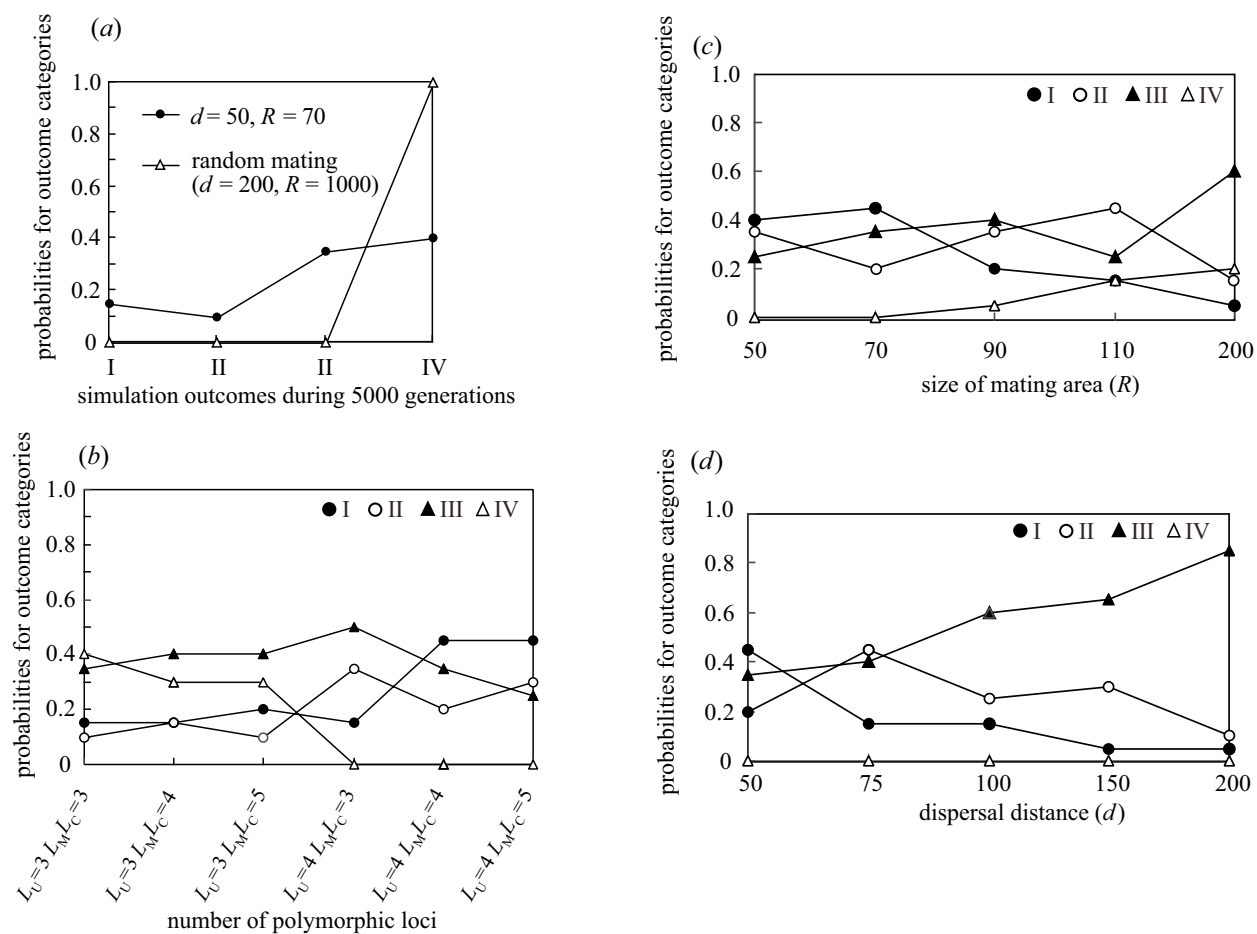


Figure 5. The effects of different initial numbers of polymorphic loci (b), the size of mating area (c) and dispersal distance ((a) and (d)) on probabilities for realizing the four outcome categories (more than 20 simulations). Minimum-distance model: (a) $W=700, r=1.6, L_U=3, L_M L_C=3$; (b) $W=700, r=1.6, d=50, R=70$; (c) $d=50, W=700, r=1.6$; (d) $R=70, W=700 \times 700, r=1.6$. Abbreviations: L_U , initial number of loci for resource-use; L_M , number of loci for the male sexual trait; L_C , initial number of loci for female preference; R1, resource distribution; I, complete speciation; II, incomplete speciation; III, monomodal resource; IV, monomorphic resource use.

(c) The effects of parameter changes on the probability of speciation and resource polymorphism

In later analyses, the effects of parameter changes on the speciation probability were examined for parameters other than the initial number of resource-use loci, female preference and male sexual traits, which in each case was set at four. For example, the effects of change in the size of mating area (R) and dispersal distance (d) on the evolution of resource use and reproductive isolation are shown in figure 5c,d. Increase in both of these factors increases the within-population dispersal of genes, which facilitates the ability of recombination to keep the genetic content of the population homogenized and destroy any association between alleles for adaptation and alleles for assortative mating that natural selection might create (Felsenstein 1981; Rice & Hostert 1993). Hence, the probability of complete speciation (I) decreased, but that of monomorphic resource use (IV) increased with increasing size of mating area; and with increasing dispersal distance, the probability of complete speciation (I) also decreased, and the monomodal resource polymorphism (III) increased.

The probabilities of speciation for different mating tac-

tics are shown in figure 6a. For all three mating tactics (no reproduction, no preference and choice for resource use), complete speciation (I) could not occur. Especially for the 'no-reproduction' tactic and the 'no-preference' tactic, the range of female preference (C) evolved to large values (III and IV), so that no change in mean female preference evolved.

Figure 6 shows the effects of resource distribution ($R1, R2$ and $R3$ in figure 2c) on probabilities for realizing the four outcome categories. The probability of speciation was highest when the amount of intermediate food resource was intermediately low ($R1$). When the amount of intermediate food resource was high ($R2$), monomodal resource polymorphism (III) frequently occurred. When the amount of intermediate food resource was low ($R3$), a subpopulation of individuals using the larger size of food did not arise (IV).

When individuals could use more than one food type, small genetic neighbourhood size augmented complete (I) or incomplete speciation (II), which was similar to the results for individuals using only one food type. In addition, resource-use phenotype evolved by diverging to the values of the two sets of most abundant food types (cf. electronic Appendix A).

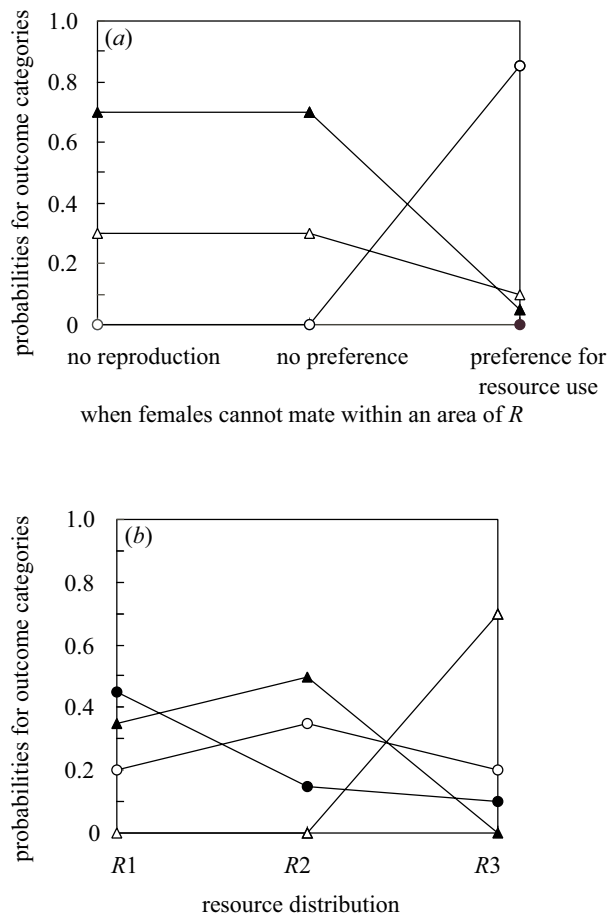


Figure 6. The effects of mating tactics and resource distribution on probabilities for realizing the four outcome categories. The initial number of resource-use loci, male sexual trait and female preference was 4. (a) $d = 50$, $R = 50$, $W = 700$, $r = 1.6$, resource distribution = R1; (b) minimum-distance model $d = 50$, $R = 70$, $W = 700$, $r = 1.6$. Black circles, (I) complete speciation; white circles, (II) incomplete speciation; black triangles, (III) monomodal resource polymorphism; white triangles, (IV) monomorphic resource use.

4. DISCUSSION

(a) Conditions for sympatric speciation

A model was used to examine the population dynamics of invasion of a vacant niche, and that of the possible, subsequent process of sympatric speciation. In the model, the vacant niche is coextensive with a niche the population has already filled, and if a subsequent process of speciation occurs, it does so even though the diverging subpopulations remain spatially coextensive within the habitat of the original population. Within the space occupied by the habitat, individuals are essentially randomly and continuously distributed, and resources are randomly distributed. Even though individuals with the same or similar values of phenotypes tend to be contiguously distributed, nevertheless individuals that used smaller food sizes and that used larger food sizes were interspersed within neighbourhoods (cf. electronic Appendix B). In other words, there is a tendency for clumping of similar types and, at the same time, a tendency for the extreme types to be interspersed.

Sympatric speciation is defined as mode of non-

allopatric speciation, which occurs in the absence of geographical isolation, when sister species evolve within the dispersal range of the offspring of a single deme (Bush 1998). In the simulation models of this study, the dispersal range of offspring was small, and individuals did not all share the same area for food searching, nor the same area for mate seeking—neither because of genotype differences, nor as the consequence of genetic isolating mechanisms. However, at the same time, because home ranges and mate searching areas for individuals extensively overlap, the mode of speciation is certainly not allopatric, nor simply parapatric. In fact, because ecological circumstances and the composition of types of individuals is essentially the same throughout the entire habitat, and seem to remain so in the process of speciation, the speciation that occurred for the simulations of this study may well be *essentially* strictly sympatric, and could probably be shown to be so.

(b) The effects of initial variation of phenotypes

The present study shows that when the initial variation of resource use is small (i.e. the initial number of resource-use loci is less than four), and the genetic neighbourhood size is large (i.e. the mating area and dispersal distance are large), then individuals cannot evolve to invade a new niche space (larger food sizes). However, if the genetic neighbourhood size is small (i.e. mating is local, and the dispersal distance is small), individuals can evolve to use an unexploited type of food resource (larger food sizes), and this sometimes leads to reproductive isolation between two diverging subpopulations: one using the original type of food resource (smaller food sizes), and the other, the previously unexploited type (larger food sizes).

When the initial variation of resource use is large (i.e. the initial number of resource-use loci is four), individuals can evolve to use larger food sizes, even when the mating area for individuals encompasses the whole habitat. However, divergence of female preference did not evolve, resulting in mating being essentially random and unassociated with resource-use phenotypes and male sexual traits. By contrast, when the genetic neighbourhood size was small ($d = 50$ and $R = 70$), the evolution of reproductive isolation between the individuals using smaller food sizes and those using larger food sizes (completed speciation I) was a frequent outcome.

(c) The effects of genetic neighbourhood size on vacant niche invasion and subsequent sympatric speciation

When the intermediate sizes of food were rare, a subpopulation of individuals using the larger food sizes did not arise; the probable reason being that even if a few mutant individuals using larger food sizes should arise, their likelihood of mating with individuals using smaller food sizes would be extremely high. Consequently, most of their offspring use intermediate sizes of food, and so their fitness decreases because there are few intermediate sizes of foods.

However, when the initial variation for resource use is large, the individuals that initially use larger food resources can mate with each other so that resource polymorphism can be maintained. Nevertheless, as recombination might destroy the association between alleles for

resource use and alleles for female mating preference, reproductive isolation could not evolve when the genetic neighbourhood size was large. When the genetic neighbourhood size was small, however, a restricted range of phenotypic values was able to exist and sustain itself within a neighbourhood area, at least temporarily (see electronic Appendix B), which further increased the likelihood of mating between individuals with the same or similar phenotypes. This self-enhancing process probably allowed selection pressures to change in favour of linkage between resource-use loci and other characters, particularly female preference and male sexual traits, which facilitated and led to reproductive isolation. Thus, small genetic neighbourhood size promoted both the invasion of a vacant niche and subsequent speciation.

Previous sympatric speciation models consider several factors that can promote sympatric speciation, such as habitat preference and mating in the same habitat (Johnson *et al.* 1996), disruptive selection and assortative mating (Dieckmann & Doebeli 1999; Kondrashov & Kondrashov 1999), sexual selection and viability selection (Turner & Burrows 1995), sexual selection without viability selection (Higashi *et al.* 1999; Kawata & Yoshimura 2000), and mating-dependent dispersal (Payne & Krakauer 1997). The model described by Dieckmann & Doebeli (1999) assumes monomodal resource distribution and strong disruptive selection by competition. Kondrashov & Kondrashov (1999) consider the possibility that the original species invades a vacant niche, and invading individuals become reproductively isolated from the original species. However, in their model, disruptive selection for ecological traits (e.g. resource use) is assumed to favour the most extreme phenotypes. Assuming a more realistic resource distribution than Kondrashov & Kondrashov's (1999) model, we have shown that large genetic neighbourhood size (approaching random mating within the region covered by the habitat) cannot lead to the invasion of a vacant niche and speciation when the vacant niche within the habitat is coextensive and interspersed with a niche already filled by a population.

(d) *Resource distribution and speciation*

These results also imply, importantly, that when intermediate resources are very rare (R_2 in figure 2), the initial population cannot invade a new niche (figure 6), but when intermediate resources are relatively abundant, a population can subdivide into subpopulations of individuals using resources at the two ends of a spectrum, and the subpopulations can coexist without speciation occurring (e.g. R_3 in figures 2 and 6). Thus, both sympatric invasion of a vacant niche and subsequent sympatric speciation will probably evolve when the amount of intermediate size of food is moderately low.

According to the previous sympatric speciation and reinforcement models, speciation might evolve more frequently when strong disruptive selection occurs (Liou & Price 1994; Dieckmann & Doebeli 1999; Kondrashov & Kondrashov 1999). However, sufficiently strong pressure for disruptive selection, as when intermediate resources are sufficiently scarce, deters sympatric invasion of a vacant niche and subsequent splitting into two sister species.

(e) *Mating tactics and female preference*

Speciation was most probable when the mating tactics were that of 'minimum distance' (females choose the nearest mates with appropriate M values if there are no appropriate mates within the mating area). Speciation did not occur for the 'no-reproduction' and 'no-choice' models. These two models assume that female choice has a cost when there are no appropriate males within the mating area. Pomiankowski *et al.* (1991) suggested that runaway sexual selection does not cause the exaggeration of male sexual traits if female preference carries a cost. Accordingly, in the present simulation, the cost of female preference might cause the range of female preference to increase. In our simulations that used the 'choice for resource use' mating tactic for females, speciation was not observed. When individuals use only one food type, individuals that use the least abundant type could survive even though the number of these individuals was small (figure 3). Thus, females that prefer males using the least abundant type remained, but this might not lead to complete speciation.

Many models of premating isolation have assumed that female preference or assortative mating is a fixed character already present as an initial condition. Later, the evolution of change in male phenotypes and female preference (i.e. which male phenotypes a female tends to choose) was examined (except for the model reported by Dieckmann & Doebeli (1999)). The model in this study examines the possibility of evolution in the degree of female preference (the range of preference), and the role of such evolution in reproductive isolation. The results suggest that when both the range of preference and female preference can evolve, speciation becomes more difficult. For instance, when the range of preference was set at a small fixed value (i.e. less than 1) for a simulation, speciation could occur, even when there was no disruptive selection (Kawata & Yoshimura 2001).

(f) *Stable resource polymorphism*

As evolutionists often have reason to consider adaptation to novel resources or empty niches, several models describing the dynamics of invasion of empty niches exist (Wilson & Turelli 1986; Johnson & Gullberg 1998). These models show that unexploited niches can be invaded by a mutant morph and that stable resource polymorphism can be maintained by density- and frequency-dependent selection or habitat-specific selection (Wilson & Turelli 1986; Johnson & Gullberg 1998). In contrast to previous models, the present model is individual-based, and assumes that resource use is polygenic. In previous mathematical or numerical models, even if the frequency of genotypes using new resources is rare, they can exist in very low frequency, because the models assumed a large population size. However, in this individual-based model, when only a few individuals use new resources, they disappear easily in the next generation by mating with individuals using old resources. Thus, when the initial variations of resource-use phenotype are small, they cannot invade new resources. However, once individuals using new resources appear, subpopulations of these individuals are stably maintained, since the present model assumes that individuals using larger sizes of food resources survive to produce young independently of the

number of individuals using a smaller size of food resource.

Resource-based polymorphism is widespread, and morphs have often evolved and coexisted in sympatry (Skilason & Smith 1995). Recent studies also suggest that natural selection caused by shifts in ecology or invasions of new habitats can drive divergence extremely fast (Carroll *et al.* 1997; Losos *et al.* 1997; Orr & Smith 1998; Schluter 1998). However, whether or not both the invasion of new niches and speciation occur for a population in the same habitat is uncertain. The simulations in this study predict that when a vacant niche is coextensive and interspersed with a niche already filled by a population, both ecological divergence and speciation within the same habitat are difficult to achieve unless the genetic neighbourhood size is small. Thus, the model predicts that populations of organisms that move within a small area, such as snails (Johannesson *et al.* 1995; Chiba 1999), are especially capable of evolving to invade new resources and to proceed then to speciate.

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