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DYNAMICS OF SPECIATION AND DIVERSIFICATION IN A METAPOPULATION

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Abstract.—We develop a simple framework for modeling speciation and diversification as a continuous process of accumulation of genetic (or morphological) differences accompanied by species and subpopulation extinction and/or range expansion. This framework can be used to approach a number of questions such as species-area distribution, species–range size distribution, the rate of ecological turnover, asymmetries of range division between sister species, waiting time until speciation and extinction, the relationship between the geographic range size and the probability of speciation, the relationships between subpopulation-level parameters and metapopulation-level parameters, and the effects of taxonomic level on these rates, distributions, and parameters. We illustrate some of these applications using numerical simulations. We develop approximations describing the dependence of the number of different taxonomic units, their average range size, and the rate of their turnover on the system size, the rate of fixation of genetic (or morphological) changes in local demes, and the rate of local extinction and colonization.

Key words.—Diversification, mathematical modeling, metapopulation, speciation.

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Most species are subdivided into a large number of local subpopulations that often have small sizes. These local subpopulations frequently become extinct and are recolonized from other locations (Simberloff 1976; Wright 1978, ch. 2; Schoener 1983; Lande 1984). Analysis of ecological and evolutionary consequences of local extinction and colonization has been a focus of numerous experimental and theoretical studies (see recent reviews by Hastings and Harrison 1994; Harrison and Hastings 1996; Barton and Whitlock 1997; Hanski and Gilpin 1997; Hanski 1998). Previous work on evolutionary effects of local extinction and colonization in metapopulations has been mainly concerned with the levels of genetic variation within and between local populations, with fixation probabilities and fixation times, and with Wright's shifting balance theory (e.g., Wright 1940; Levins 1970; Slatkin 1977; Slatkin and Wade 1978; Wade 1978; Lande 1979, 1984, 1992; Maruyama and Kimura 1980; Wade and McCauley 1988; Whitlock and McCauley 1990; Barton 1993; Michalakis and Olivieri 1993; Whitlock et al. 1993).

Here, we apply similar ideas in the context of speciation and diversification by modeling how a species occupying a range of ''patches'' breaks up into two or more new species. Understanding speciation still remains a major challenge faced by evolutionary biologists (Mayr 1982; Coyne 1992; Templeton 1994). Distinctive features of the model proposed here are that it is simple, dynamical, describes the complete process of speciation, and can be easily implemented on a computer. This model is a simplified version of that studied numerically in Gavrilets et al. (1998, 2000) and analytically in Gavrilets (1999b), which in turn represents a specific case of holey adaptive landscapes (Gavrilets 1997a,b, 2000; Gavrilets and Gravner 1997). Within this framework, speciation is a consequence of accumulating genetic differences, which is in accord with a classical view of speciation (e.g., Dobzhansky 1937; Coyne 1992; Wu and Palopoli 1994). A new element of the current work is that we consider not just a single act of speciation, but rather a continuous process of species splitting into two or more new species followed by range expansion and/or extinction. Our approach is closely related to several previous studies. In particular, Orr and Orr (1996) and Gavrilets (1999b) modeled allopatric speciation without considering extinction and colonization. These two-processes were not included by Manzo and Peliti (1994), Gavrilets et al. (1998, 2000), and Gavrilets (1999b) in their models of parapatric speciation. Bramson et al. (1996, 1998), Durrett and Levin (1996), and Allmon et al. (1998) modeled the process of extinction and speciation in a metapopulation, but did not consider the degree of genetic divergence between subpopulations. Our approach complements these previous studies by simultaneously considering both the process of the accumulation of genetic differences between subpopulations that leads to speciation and diversification and the process of extinction and colonization of local demes that leads to species extinction or expansion.

Our model can be used to approach a number of questions that have been extensively discussed in the literature. These questions include species-area distribution (e.g., Connor and McCoy 1979; Rosenzweig 1995), species–range size distribution (e.g., Gaston 1996, 1998; Gavrilets et al. 2000), the rate of ecological turnover (e.g., Russell 1998), asymmetries of range division between sister species (e.g., Brown 1957; Mayr 1963; Lynch 1989; Frey 1993; Rosenzweig 1995; Wagner and Erwin 1995; Chown 1997; Gavrilets et al. 1998, 2000), waiting time until speciation (e.g., Orr and Orr 1996; Gavrilets at al. 1998, 2000) and extinction, the relationship between the geographic range size and the probability of speciation (e.g., Stanley 1986, 1990; Gavrilets et al. 1998, 2000), dynamics of adaptive radiations (e.g., Schluter 1998), the relationships between subpopulation-level parameters and metapopulation-level parameters, and the effects of taxonomic order on these rates, distributions, and parameters. We will illustrate most of these applications below. In addition, insights provided by models that describe the splitting of geographic space between sister species may be useful for thinking about the way species partition other resources (e.g., Sugihara 1980; Nee et al. 1991; Takeshi 1993). Finally, the development of theoretical models focusing on the dynamics of speciation in spatially distributed populations would complement data analyses focusing on spatial aspects of molecular processes leading to speciation (e.g., Avise et al. 1987; Avise 1994; Barraclough and Vogel 2000).

In developing the model described below, we will follow the classical metapopulation approach (Levins 1970; see review by Hanski 1991) by neglecting effects of migration in extant demes. This approach can be questioned on several grounds (e.g., Stacey et al. 1997). However, as emphasized by Hanski (1997), first, it is too early to conclude that classical Levins-type metapopulations are exceptional, and, second, a better understanding of the classical case is necessary for enhancing our understanding of metapopulation dynamics in more general situations. Our modeling approach will imply that in the absence of extinction the demes would continuously accumulate new mutations and diverge genetically (cf. Orr and Orr 1996). As a working example, we envision a plant metapopulation where local demes produce a large number of seeds of which only few germinate. In this case, migrant seeds will have extremely small probability of germinating unless there is an extinction event eliminating all or most resident plants. Genetic consequences of migration into extant demes can be neglected only if the rate of migration is small. However, this rate does not have to be extremely small. Individual-based simulations and analytical approximations (Gavrilets et al. 1998, 2000; Gavrilets 1999b) show that continuous genetic divergence can be initiated even when neighboring demes exchange as many as one to three individuals per generation. With low levels of gene flow relative to the rate of extinction and recolonization, the level of genetic divergence of local populations is controlled by the latter rate (Slatkin 1977; Lande 1992). Here, it is the extinction and recolonization process, rather than migration, that will prevent the infinite divergence of local populations.

MODEL

We consider a habitat subdivided into discrete ''patches,'' each of which can support a finite number of individuals. The patches are inhabited by populations with discrete and nonoverlapping generations (one population per patch). We assume that reproduction involves gene exchange (amphimixis) between individuals and that there is a large number of possibly linked loci potentially affecting reproductive isolation.

System State

Here, we will be interested in the level of genetic divergence between subpopulations in a specific set of genes. This can be characterized in terms of genetic distance, d, between pairs of individuals defined as the number of single locus substitutions (mutational steps) separating two individuals. For a moment, we do not specify the loci over which d is computed. If there are only two alleles per locus, d is just the number of loci at which two individuals are different. Consider two patches, the ith and jth. Let D_{ij} be the average genetic distance between subpopulations at patches i and j defined as the average of genetic distances, d, between pairs of individuals from these two patches. In what follows the state of a system with n patches will be characterized by a symmetric $n \times n$ matrix $\mathbf{D} = \{D_{ij}\}$ $(1 \leq i, j \leq n)$ of average genetic distances between pairs of subpopulations. The diagonal elements of this matrix characterize the level of genetic variation within demes. Below, we will assume these elements to be maintained at an approximately constant level D_w by a balance of selection, mutation, drift and other factors.

Mutation

At each time step, a mutation can be fixed in each deme with probability μ. (The dependence of μ on population size, mutation and migration rates, effects of reproductive isolation, selection for local adaptation, and other factors is discussed for a specific model in Gavrilets 1999b.) The probability μ is assumed to be small, whereas the number of possible mutations is large so that each mutation that is fixed in a deme is new to the system. Thus, if a new mutation is fixed in deme i, all average genetic distances to this deme increase by one:

$$D_{ij} \rightarrow D_{ij} + 1 \text{ for all } j \neq i. \tag{1}$$

Extinction and Colonization

At each time step, each population may go extinct with a small probability δ. Immediately after extinction, the deme is colonized by individuals from one of the ''neighboring'' nonextinct demes. (The assumption that colonization happens immediately after extinction is not a serious limitation of the approach [see Durrett and Levin 1996].) Following previous work (e.g., Slatkin and Wade 1978; Lande 1992), we assume that newly founded populations increase to carrying capacity in one generation. Thus, if deme i goes extinct and is colonized from deme i^*, the average genetic distances to deme i are substituted by average genetic distances to deme i^*:

$$D_{ij} \rightarrow D_{i^*j} \text{ for all } j \neq i. \tag{2}$$

Reproductive Isolation and Species

The set of genes over which genetic distance, d, is computed will represent the loci affecting viability, fertility, and mating behavior. We assume that reproductive isolation is caused by cumulative genetic change in these loci. We will use a very simple symmetric model (Gavrilets et al. 1998, 2000; Gavrilets 1999b; cf. Higgs and Derrida 1992) that allows one to treat both pre- and postmating isolation within the same framework. We posit that an encounter of two individuals can result in viable and fecund offspring only if the individuals are different by no more than K mutational steps. Otherwise the individuals do not mate (premating reproductive isolation) or these offspring are inviable or sterile (postmating reproductive isolation). In this formulation, any two genotypes different by more than K mutational steps can be conceptualized as sitting on opposite sides of a hole in a holey adaptive landscape (Gavrilets 1997a,b, 2000; Gavrilets and Gravner 1997; Gavrilets et al. 1998). At the same time, a population can evolve to any reproductively isolated state by a chain of single-locus substitutions. Two individuals are reproductively isolated if the genetic distance between them is larger than K. Two subpopulations are completely reproductively isolated if the minimum genetic distance between individuals coming from different populations is larger than K. A criterion for reproductive isolation of populations i and j that will be used below is $D_{ij} > K' \equiv K + \Delta$ with some positive Δ that depends on the level of within-population variation. Using a sufficiently large Δ will almost certainly guarantee that no genetic distance between individuals from different subpopulations is smaller than K. Appropriate values of Δ can be approximated analytically (see Gavrilets 1999b). In what follows, we will use K (i.e., drop the prime in K'). We will define a species as a continuous chain of patches formed by pairs of demes that are not reproductively isolated. This definition implies that if demes i and j are not reproductively isolated ($D_{ij} \leq K$) and demes j and k are not reproductively isolated ($D_{jk} \leq K$), then all three demes belong to the same species, even if demes i and k are reproductively isolated ($D_{ik} > K$). This definition is analogous to that one used in the single linkage clustering technique (e.g., Everitt 1993). It would treat all demes forming a ring species (e.g., Mayr 1942, 1963; Wake 1997) as belonging to a single biological species. Note that here it is not continuous gene flow, but common ancestry that ''keeps'' a species together.

Numerical Algorithm

It is very easy to simulate the model dynamics numerically. One starts with an initial matrix **D**. For example, one can choose a matrix with all diagonal and nondiagonal elements equal to D_w, which would correspond to a single species. (Initial conditions are not important as far as the final stochastic state is concerned.) Then, for each generation do the following: For each deme decide whether it fixes a new mutation (with probability μ) or not (with probability $1 - \mu$). Update the elements of matrix **D** for the demes that have fixed new mutations using equation (1). For each deme decide whether it goes extinct (with probability δ) or not (with probability $1 - \delta$). For each deme that goes extinct randomly pick up a ''neighboring,'' nonextinct deme from which the colonization will take place. Update the corresponding elements of matrix **D** using equation (2).

Graphical Output and Statistics

Let us assume that the demes are linearly arranged (as in the linear stepping-stone model; Kimura and Weiss 1964) and that colonization occurs from one of the two nearest neighboring demes. A common method for visualizing the state of one- and two-dimensional stepping-stone systems is to use different colors to represent the state of patches. Here, instead of concentrating on individual demes we focus on the differences between pairs of neighboring demes. We use linearly arranged along the x-coordinate colored pixels to represent the average genetic distances between neighboring demes. For example, a pixel at position i will represent the average genetic distance between demes i and $i + 1$. We use the y-coordinate for time variable. If one is mainly interested in the dynamics of species borders, only two colors need to be used: one for the distances smaller or equal to K and another for the distances larger than K. The latter color will represent species borders (see Fig. 1). However, one can get additional information by using more colors. For example, one can use colors from red to orange to yellow to green to blue to purple to represent a continuum of distances from $\mathbf{D} = D_w$ to $\mathbf{D} = K$ (see a color figure at www.tiem.utk.edu/~gavrila/PAPS/meta-fig.html). Here, different colors would correspond to different levels of genetic divergence (within species and/or between species). This graphical output represents a very powerful method for training intuition about the dynamic behavior of the model studied here. Additionally, a set of different statistics can be computed, such as the number of species (counted by the number of borders), the distribution of species ranges, the distributions of the time to speciation and extinction, and the distribution of the relative ranges of the two sister species a species splits.

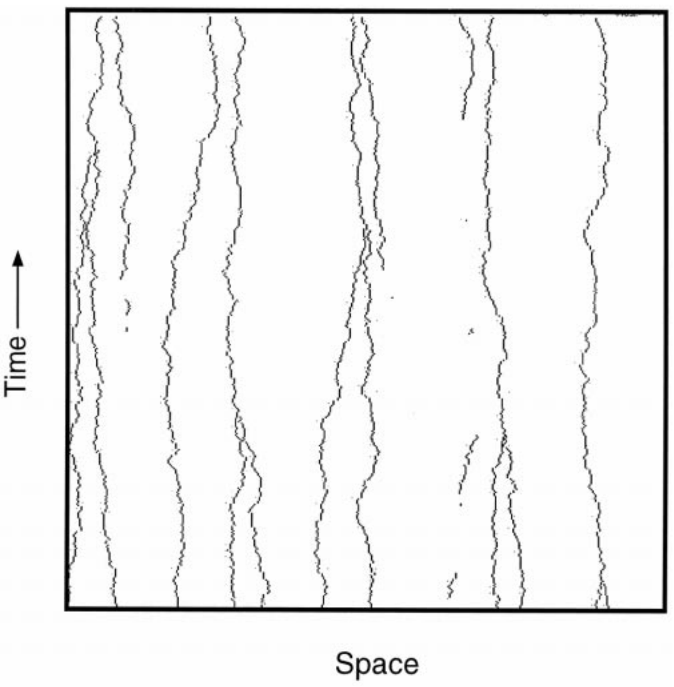

FIG. 1. The dynamics of species borders. The horizontal axes represents spatial dimension. The vertical axes represents time (about 6000 generations). The lines represent species borders. Data are plotted every 20th time step. The emergence of several new borders (representing speciation) as well as several border collisions (representing extinction) and border disappearances are observed. Parameters are $n = 400$, $\mu = 0.001$, $\delta = 0.06$, $K = 20$.

NUMERICAL AND ANALYTICAL RESULTS

We consider a system of n demes arranged on a circle. (This allows one to exclude boundary effects.) We start by-reporting some numerical results and then give analytical approximations for three important characteristics of system dynamics.

While running the model numerically, one observes a continuous process of emergence, random movement, collision, and annihilation of borders (see Fig. 1). A new border can appear after a mutation in a deme, after extinction of an ''intermediate'' deme (or a chain of adjacent demes), or after a collision of two borders. (We treat borders that appear from collision as new borders.) Borders disappear in isolation or

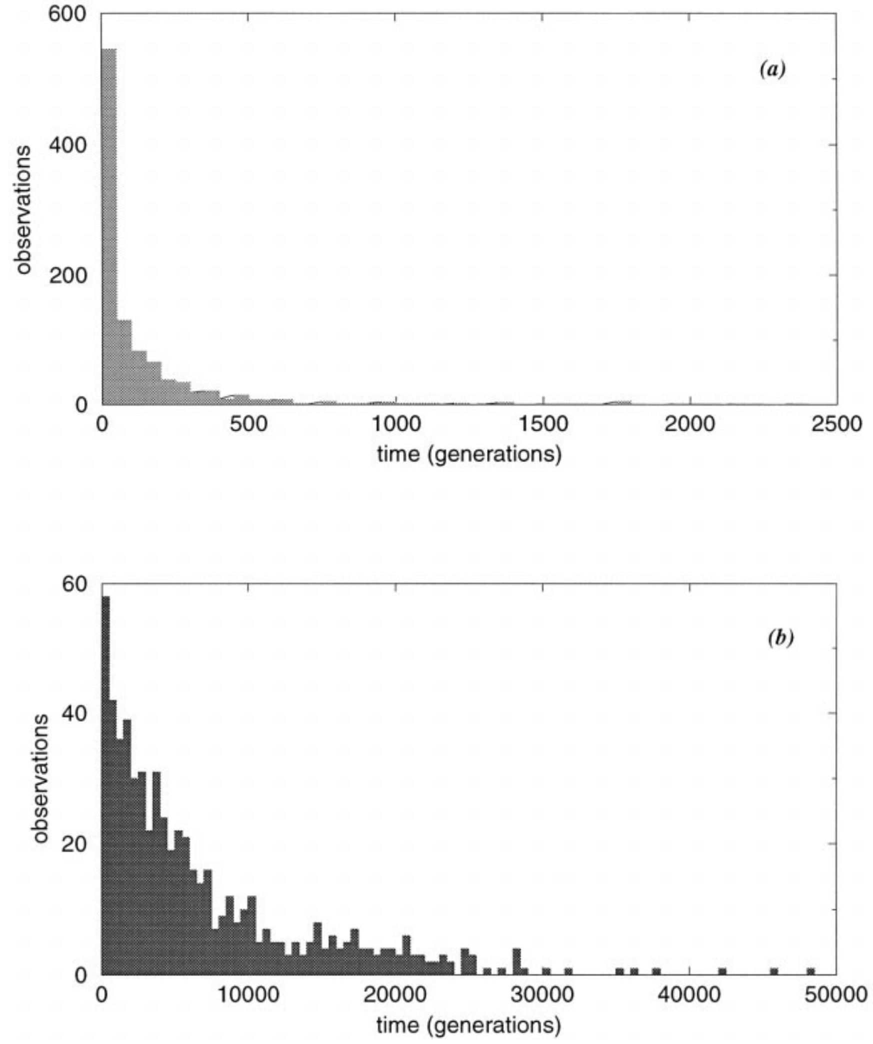

FIG. 2. The distribution of the life span of borders. Parameters are $n = 400$; $K = 20$; $\mu = 0.001$; $\delta = 0.04$. (a) Borders that appear and disappear in isolation. (b) Borders that appear in isolation and disappear in collision.

as a result of border collision. The former case happens when a deme has significantly diverged from one of its two nearest neighbors, but the right and left neighbors, although isolated geographically, are still similar genetically. In this case, the extinction of the middle deme will result in border disappearance. Such borders can be interpreted as representing speciation events that were not successful. In the case of border collision, all demes between two neighboring borders go extinct simultaneously. We interpret such events as ''species extinction.''

From watching the model dynamics on the computer screen, it is apparent that the life span of borders that appear and disappear in isolation is much shorter than the life span of borders that disappear in collisions. Figures 2a and 2b make this point more precise.

Figure 3 illustrates the changes in the number of borders during 10^6 generations. The number of unsuccessful speciation events (characterized by the number of borders that disappear in isolation) is larger than the number of ''real'' speciation events (characterized by the number of borders that disappear in collision). However, because the former have relatively short life spans they will not contribute significantly to the average number of borders. Thus, the average number of species, S (over a long time interval), can be estimated by the average number of borders.

Figure 4 illustrates the distribution of species range size. The data for this figure were collected over the interval from generation 50,000 to generation 1,050,000 by sampling every 1000th generation. This distribution is right-skewed on the linear scale (Fig. 4a) and becomes left-skewed on the log-scale (Fig. 4b). These properties are similar to those of the species-range distributions estimated from real data (e.g., Gaston 1996, 1998). Species are more likely to break at the center of their range (Fig. 5; cf. Gavrilets et al. 1998, 2000). The larger the species range, the more likely it will break. However, because there are not many species with very large range sizes (see Fig. 4), the species that contribute the largest number of new species are those with intermediate range sizes (Fig. 6).

Simple analytical approximations can be used to evaluate the dependence of some important dynamical characteristics of the model on parameters (see Appendix for details). The

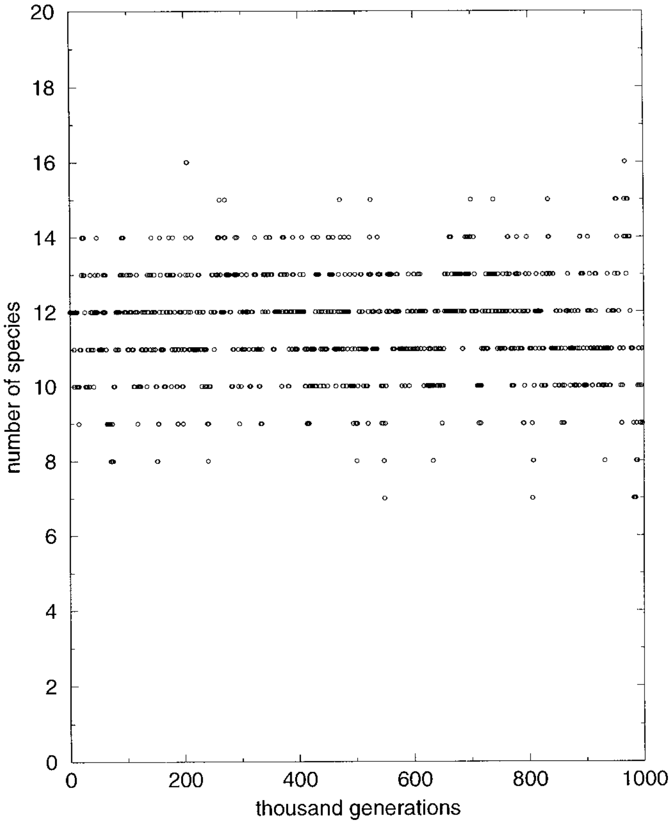

FIG. 3. The number of species (borders) during 10^6 generations. The datapoints were sampled every 1000th generation. Parameters are the same as in Figure 2.

formulae given below assume that the mutation rate is much smaller than the extinction/colonization rate, which is small, and that the number of genetic differences necessary for speciation is sufficiently high ($\mu << \delta << 1 << K$). The average range size, R, of a species (that is the number of demes between two neighboring borders) is

$$R = \sqrt{\frac{\pi}{2}\frac{\delta K}{\mu}}. \tag{3}$$

The average number of species, S, in the system is

$$S = \sqrt{\frac{2}{\pi}\frac{\mu}{\delta K}}n. \tag{4}$$

Note that $S = n/R$. The average turnover rate, T, can be defined as the number of species extinctions per unit time interval per the number of species present (e.g., Russell 1998). Here, species extinction is represented by the collision of two species borders. The turnover rate is

$$T = \frac{\mu}{K}. \tag{5}$$

To check these analytical approximations and to get further insights into the model dynamics, we performed numerical simulations. The following is a list of parameter values used: $\mu = 0.01, 0.001, 0.0001$; $\delta = 0.01, 0.02, 0.04, 0.16$; $K = 10, 20, 40, 80$; and $n = 100, 200, 400, 800$. We considered all 192 ($3 \times 4 \times 4 \times 4$) possible combinations of parameters. The match of theoretical predictions and numerical estimates computed overthe interval from generation 50,000 to generation 550,000 is very good. In most cases, equation (4) underestimates the average number of species by ~2%, whereas equation (5) overestimates the turnover rate by about 5–10%. In the case of the smallest mutation rate ($\mu = 0.0001$), the errors are slightly higher.

DISCUSSION

Here, we have studied speciation as a continuous process of accumulation of genetic differences accompanied by species and subpopulation extinction and/or range expansion. In our model, reproductive isolation is a consequence of cumulative genetic divergence over a large set of loci potentially affecting viability, fertility, or mating behavior (e.g., Wu and Palopoli 1994; Naveira and Masida 1998). Alternatively, hybrid sterility or inviability can result from incompatibility of few ''complementary'' genes as modeled by Orr (1995; Orr and Orr 1996). In both approaches, a population can evolve from one state to a reproductively isolated state along a ''ridge'' of well-fit genotypes without any maladaptive steps, as first suggested by Bateman (cited in Orr 1997) and Dobzhansky (1937). Note that the existence of such ''ridges'' is a general feature of multidimensional adaptive landscapes (Gavrilets and Gravner 1997; Gavrilets 1997a, 2000), rather than a property of a specific genetic architecture. For simplicity, we assumed that the state of no reproductive isolation changes to complete reproductive isolation when genetic divergence exceeds some threshold. Other types of genetic architecture can result in a gradual accumulation of reproductive isolation. For example, in Orr's (1995) model reproductive isolation increases faster than linearly in time (the ''snowball effect''), whereas in a classical model of viability selection with between-locus multiplicativity and weak within-locus underdominance a ''slowdown'' is observed (Walsh 1982). However, for the problems we approach here, whether reproductive isolation appears suddenly or accumulates gradually is largely irrelevant.

The main application of the mathematical model we have developed is to provide new insights, to train intuition and make it more precise, and to identify key components in the complex process of speciation in metapopulations. Intuition tells one that increasing the rate of fixation of new mutations should increase the rate of speciation increasing the number of species in the system. Decreasing the rate of extinction-colonization should have a similar effect because larger levels of genetic variation will accumulate in the system. Our results make this intuition more precise by demonstrating that actual dependence is square-root (see eqs. 3 and 4). For example, changing δ or μ by a factor of four will result in a change in the number of species and the average range size by a factor of two. These results provide a formal justification for the idea that species can accumulate rapidly after colonizing a new environment if local populations in the novel environment have a reduced probability of extinction (e.g., Mayr 1963; Allmon 1992; Schluter 1998). A somewhat counterintuitive prediction is that the turnover rate, T, does not depend on the deme extinction-colonization rate, δ (see eq. 5).

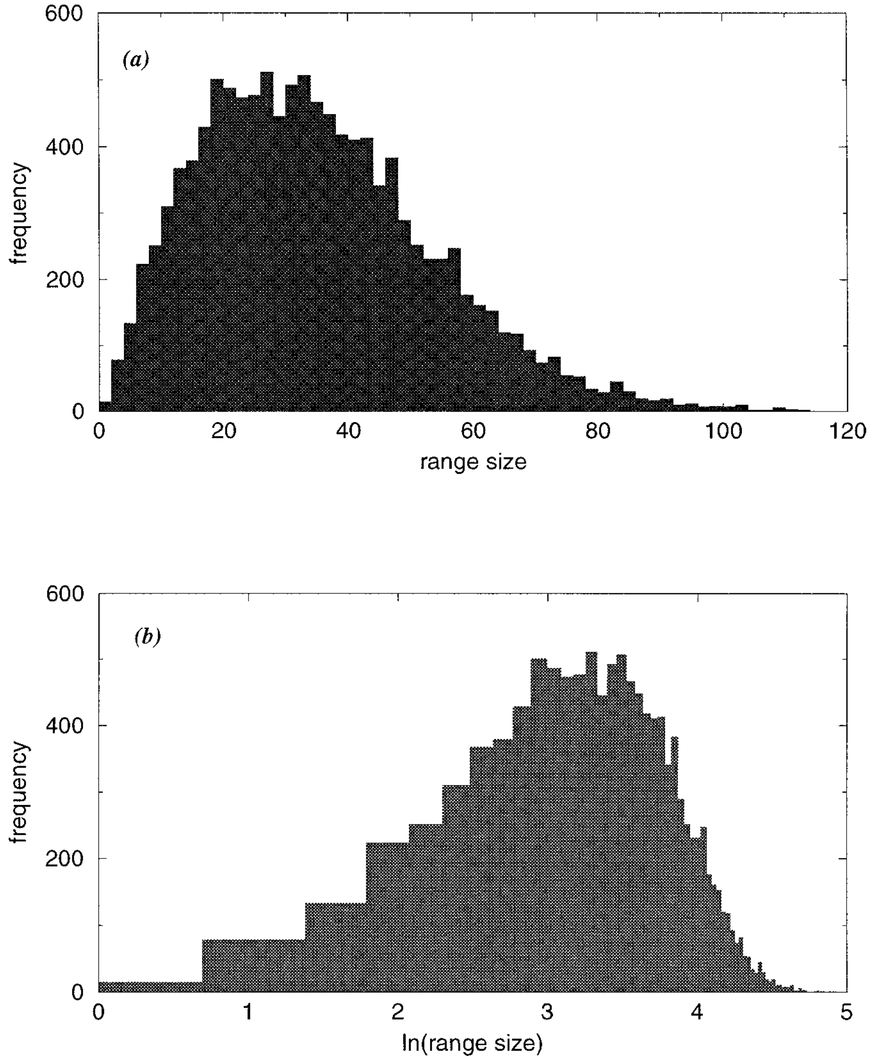

FIG. 4. The species–range size distribution: (a) Linear scale; and (b) logarithmic scale. Parameters are the same as in Figure 2.

This happens because the increase in the extinction rate resulting from an increase in δ is exactly balanced by a decrease in the number of species, S, maintained in the system. The model produces a species–range size distribution similar to those deduced from data (e.g., Gaston 1996, 1998) and exponential distributions of life-span of species and borders between them. The model shows that there is a large number of unsuccessful speciation events in which a deme may significantly diverge from one of its neighbors (which both stay similar), but then go extinct, resulting in reconstructing the continuity in a species range. For discussion of species-area curves in similar two-dimensional systems with $K = 1$, see Bramson et al. (1996) and Durrett and Levin (1996).

An important parameter of our model is K, which was introduced above as a minimum genetic divergence required for reproductive isolation. Intuition suggests that increasing K should result in decreasing the number of species. In our model, the exact dependence is $1/\sqrt{K}$-type. The model also shows that the rate of species turnover should decrease as $1/K$. This results in that in clades with, say, four times as many genetic changes required for speciation, there will be only half as many species and the turnover rate will be one-fourth of that in a reference clade.

The model was developed for sexual species. However, because reproductive isolation is treated as a by-product of genetic divergence, the framework can be used for modeling the dynamics of speciation in asexual species. In this case the criterion for assigning different demes to different or the same species will be the degree of genetic divergence between them. Moreover, our framework can be used for modeling both genetic divergence and morphological divergence. In this case, the matrix of pairwise distances between demes will represent ''morphological'' distance defined as an average number of morphological traits at that the corresponding subpopulations differ (for an application of this approach to a paleontological dataset, see Gavrilets 1999a).

There is an alternative interpretation of parameter K relevant for both sexual and asexual species as well as for the case of morphological distances. It is important to realize that changing this parameter does not change the system state (which is described by a matrix of pairwise distances) or dynamics. What is affected by K is the graphical output and

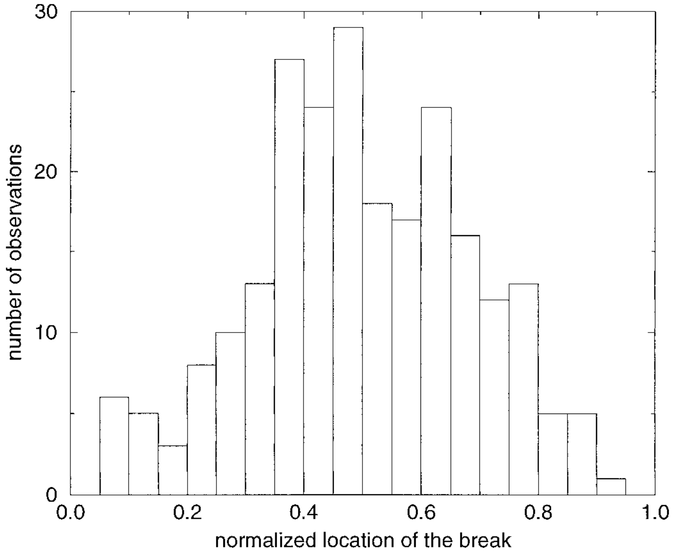

FIG. 5. The distribution of the location of the break relative to the ancestral species range. For an ancestral species splitting in proportions *x:y*, the normalized location of the break is defined as *x*/(*x* + *y*). Parameters are the same as in Figure 2.

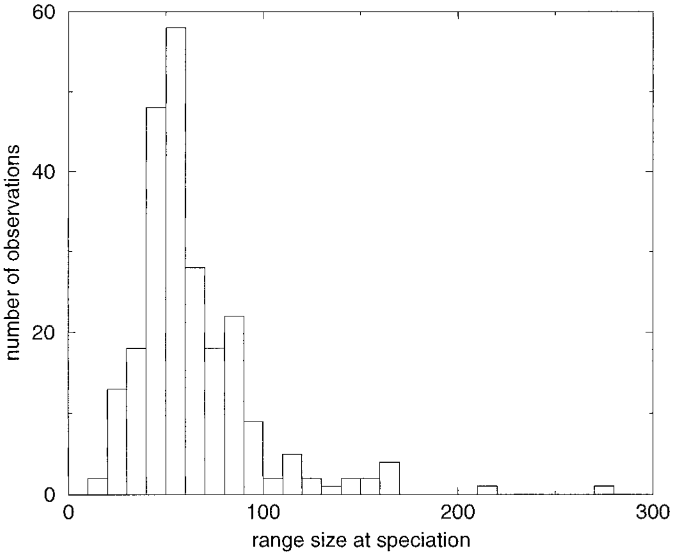

FIG. 6. The distribution of the species ranges at speciation. Parameters are the same as in Figure 2.

the corresponding interpretation of the model behavior. Parameter K can be thought of as a measure of taxonomic level. For example, let us specify an increasing sequence of K-values: $K_1 < K_2 < K_3 \ldots$. Then, all demes at genetic (or morphological) distance K_1 or less can be thought of as belonging to the same species, all demes at genetic (or morphological) distance larger than K_1 but not larger than K_2 can be thought of as belonging to different species within the same genus, all demes at genetic (or morphological) distance larger than K_2 but smaller or equal to K_3 can be thought of as belonging to different species and genera within the same family, etc. This approach allows one to study the dynamics of the hierarchical structure of the metapopulation. Using this interpretation, equations (4) and (5) show that both the number of different taxonomic units and the turnover rate decrease with taxonomic level ($1/\sqrt{K}$-dependence in the former case and $1/K$-dependence in the latter case). This also leads to some interesting dependences that probably can be evaluated empirically. One prediction is that the ratio of turnover rates at two different taxonomic levels should be the inverse of the ratio of average genetic (or morphological) differences between the corresponding groups:

$$\frac{T_i}{T_j} = \frac{K_j}{K_i}. \tag{6}$$

The number of genetic (morphological) differences, K_i, may not be easy to estimate. However, the number of taxonomic units at different taxonomic levels (e.g., species within a genus or genera within a family) can be approximated (e.g., Burlando 1990). Combining equations (4) and(5) for two different taxonomic levels leads to

$$\frac{T_i}{T_j} = \left(\frac{S_j}{S_i}\right)^2. \tag{7}$$

It would be interesting to use existing paleontological data to evaluate the relationships between the turnover rates and the number of taxonomic units at different taxonomic levels, such as described by equations (6) and (7).

The model studied here has obvious limitations that will make testing predictions using real data more difficult. Among the most serious are that we consider a one-dimensional spatial arrangement of demes rather than two-dimensional, migration into occupied demes has no effects on the probability of fixing new mutations, and no more than a single population can occupy a patch. However, both the framework developed here and the insights it leads to should be helpful in developing more realistic models that would remove these limitations.

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LITERATURE CITED

Allmon, W. D. 1992. A causal analysis of stages in allopatric speciation. Oxford Survey in Evolutionary Biology 8:219–257.

Allmon, W. D., P. J. Morris, and M. L. McKinney. 1998. An intermediate disturbance hypothesis of maximal speciation. Pp. 349–376 *in* M. L. McKinney and J. A. Drake, eds. Biodiversity dynamics: turnover of populations, taxa, and communities. Columbia Univ. Press, New York.

Avise, J. C. 1994. Molecular markers, natural history and evolution. Chapman and Hall, New York.

Avise, J. C., J. Arnold, R. M. Ball Jr., E. Birmingham, T. Lamb, J. E. Neigel, C. A. Reeb, and N. C. Saunders. 1987. Intraspecific phylogeography: the mitochondrial DNA bridges between population genetics and systematics. Annu. Rev. Ecol. Syst. 18: 489–522.

Barraclough, T. G., and A. P. Vogel. 2000. Detecting the geographic pattern of speciation from species-level phylogenies. Am. Nat. 155:419–434.

Barton, N. H. 1993. The probability of fixation of a favored allele in asubdivided population. Genet. Res. 62:149–157.

Barton, N. H., and M. C. Whitlock. 1997. The evolution of metapopulations. Pp. 183–210 *in* I. Hanski and M. E. Gulpin, eds. Metapopulation biology: ecology, genetics, and evolution. Academic Press, San Diego, CA.

Bramson, M., J. T. Cox, and R. Durrett. 1996. Spatial models for species area curves. Ann. Probab. 24:1727–1751.

———. 1998. A spatial model for the abundance of species. Ann. Probab. 26:658–709.

Brown, J. L., Jr. 1957. Centrifugal speciation. Quart. Rev. Biol. 32: 247–277.

Burlando, B. 1990. The fractal dimension of taxonomic systems. J. Theor. Biol. 146:99–114.

Chown, S. L. 1997. Speciation and rarity: separating cause from consequence. Pp. 91–109 *in* W. E. Kunin and K. J. Gaston, eds. The biology of rarity. Chapman and Hall, London.

Connor, E. F., and E. D. McCoy. 1979. The statistics and biology of species-area-relations. Am. Nat. 113:791–833.

Coyne, J. A. 1992. Genetics and speciation. Nature 355:511–515.

Dobzhansky, T. G. 1937. Genetics and the origin of species. Columbia Univ. Press, New York.

Durrett, R., and S. Levin. 1996. Spatial models for species-area curves. J. Theor. Biol. 179:119–127.

Everitt, B. S. 1993. Cluster analysis. Arnold, London.

Frey, J. K. 1993. Modes of peripheral isolate formation and speciation. Syst. Biol. 42:373–381.

Gaston, K. J. 1996. Species-range-size distributions: patterns, mechanisms and implications. Trends Ecol. Evol. 11:197–201.

——— 1998. Species-range size distributions: products ofspeciation, extinction and transformation. Phil. Trans. R. Soc. Lond. B 353:219–230.

Gavrilets, S. 1997a. Evolution and speciation on holey adaptive landscapes. Trends Ecol. Evol. 12:307–312.

———. 1997b. Hybrid zones with epistatic selection of Dobzhansky type. Evolution 51:1027–1035.

———. 1999a. Dynamics of clade diversification on the morphological hypercube. Proc. R. Soc. Lond. B 266:817–824.

———. 1999b. A dynamical theory of speciation on holey adaptive landscapes. Am. Nat. 154:1–22.

———. 2000. Evolution and speciation in a hyperspace: the roles of neutrality, selection, mutation and random drift. *In* J. Crutchfield and P. Schuster, eds. Towards a comprehensive dynamics of evolution: exploring the interplay of selection, neutrality, accident, and function. Oxford Univ. Press, Oxford, U.K.

Gavrilets, S., and J. Gravner. 1997. Percolation on the fitness hypercube and the evolution of reproductive isolation. J. Theor. Biol. 184:51–64.

Gavrilets, S., H. Li, and M. D. Vose. 1998. Rapid parapatric speciation on holey adaptive landscapes. Proc. Roy. Soc. London B 265:1483–1489.

———. 2000. Patterns of parapatric speciation. Evolution 54: 1126–1134.

Hanski, I. 1991. Single-species metapopulation dynamics. Pp. 17–38 *in* M. E. Gulpin and I. Hanski, eds. Metapopulation dynamics: empirical and theoretical investigations. Academic Press, London.

———. 1997. Metapopulation dynamics: from concepts and observations to predictive models. Pp. 69–91 *in* I. Hanski and M. E. Gulpin, eds. Metapopulation biology: ecology, genetics, and evolution. Academic Press, San Diego, CA.

———. 1998. Metapopulation dynamics. Nature 396:41–49.

Hanski, I., and M. E. Gilpin, eds. 1997. Metapopulation biology: ecology, genetics, and evolution. Academic Press, San Diego, CA.

Harrison, S., and A. Hastings. 1996. Genetic and evolutionary consequences of metapopulation structure. Trends Ecol. Evol. 11: 180–183.

Hastings, A., and S. Harrison. 1994. Metapopulation dynamics and genetics. Annu. Rev. Ecol. Syst. 25:167–188.

Higgs, P. G., and B. Derrida. 1992. Genetic distance and species formation in evolving populations. J. Mol. Evol. 35:454–465.

Kelly, F. P. 1977. The asymptotic behavior of an invasion process. J. Appl. Prob. 14:584–590.

Kimura, M., and G. H. Weiss. 1964. The stepping stone model of population structure and the decrease of genetic correlation with distance. Genetics 49:561–576.

Lande, R. 1979. Effective deme sizes during long-term evolution estimated from rates of chromosomal rearrangements. Evolution 33:234–251.

———. 1984. The expected fixation rate of chromosomal inversions. Evolution 38:743–752.

———. 1992. Neutral theory of quantitative genetic variation in anisland model with local extinction and colonization. Evolution 46:381–389.

Levins, R. 1970. Extinction. Lect. Math. Life Sci. 2:75–107.

Lynch, J. D. 1989. The gauge of speciation: on the frequencies of modes of speciation. Pp. 527–553 *in* D. Otte and J. A. Endler, eds. Speciation and its consequences. Sinauer, Sunderland, MA.

Manzo, F., and L. Peliti. 1994. Geographic speciation in the Derrida-Higgs model of species formation. J. Phys. A: Math. Gen. 27:7079–7086.

Maruyama, T., and M. Kimura. 1980. Genetic variability and effective population size when local extinction and colonization of subpopulations are frequent. Proc. Natl. Acad. Sci. USA 77: 6710–6714.

Mayr, E. 1942. Systematics and the origin of species. Columbia Univ. Press, New York.

———. 1963. Animal species and evolution. Belknap Press, Cambridge, MA.

———. 1982. The growth of biological thought. Harvard Univ. Press, Cambridge, MA.

Michalakis, Y., and I. Olivieri. 1993. The influence of local extinctions on the probability of fixation of chromosomal rearrangements. J. Evol. Biol. 6:153–170.

Naveira, H. F., and X. R. Masida. 1998. The genetic of hybrid male sterility in *Drosophila.* Pp. 330–338 *in* D. J. Howard and S. H. Berlocher, eds. Endless forms: species and speciation. Oxford Univ. Press, New York.

Nee, S., P. H. Harvey, and R. M. May. 1991. Lifting the veil on abundance patterns. Proc. R. Soc. Lond. B 243:161–163.

Orr, H. A. 1995. The population genetics of speciation: the evolution of hybrid incompatibilities. Genetics 139:1803–1813.

———. 1997. Dobzhansky, Bateson, and the genetics of speciation. Genetics 144:1331–1335.

Orr, H. A., and L. H. Orr. 1996. Waiting for speciation: the effect of population subdivision on the waiting time to speciation. Evolution 50:1742–1749.

Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge Univ. Press, Cambridge, U.K.

Russell, G. J. 1998. Turnover dynamics across ecological and geological scales. Pp. 377–404 *in* M. L. McKinney and J. A. Drake, eds. Biodiversity dynamics: turnover of populations, taxa, and communities. Columbia Univ. Press, New York.

Schluter, D. 1998. Ecological causes of speciation. Pp. 114–129 *in* D. J. Howard and S. H. Berlocher, eds. Endless forms. Species and speciation. Oxford Univ. Press, New York.

Schoener, T. W. 1983. Rate of species turnover decreases with from lowerto higher organisms: a review of the data. Oikos 41: 372–377.

Simberloff, D. 1976. Experimental zoogeography of islands: effects of island size. Ecology 57:629–648.

Slatkin, M. 1977. Gene flow and genetic drift in a species subject to frequent local extinction. Theor. Popul. Biol. 12:253–262.

Slatkin, M., and M. J. Wade. 1978. Group selection on a quantitative character. Proc. Natl. Acad. Sci. USA 75:3531–3534.

Stacey, P. B., V. A. Johnson, and M. L. Taper. 1997. Migration within metapopulations: the impact upon local population dynamics. Pp. 267–291 *in* I. Hanski and M. E. Gulpin, eds. Metapopulation biology: ecology, genetics, and evolution. Academic Press, San Diego, CA.

Stanley, S. M. 1986. Population size, extinction, and speciation: the fission effect in Neogene Bivalvia. Paleobiology 12:89–110.

———. 1990. Adaptive radiation and macroevolution. Pp. 1–15 *in* P. D. Taylor and G. P. Larwood, eds. Major evolutionary radiations. Clarendon Press, Oxford, U.K.

Sugihara, G. 1980. How do species divide resources? Am. Nat. 116: 770–787.

Takeshi, M. 1993. Species abundance patterns and community structure. Adv. Ecol. Res. 24:111–186.

Templeton, A. R. 1994. The role of molecular genetics inspeciation studies. Pp. 455–47 *in* B. Schierwater, B. Streit, G. P. Wagner, and R. DeSalle, eds. Molecular ecology and evolution: approaches and applications. Birkhaüser, Basel, Switzerland.

Wade, M. D. 1978. A critical review of the models of group selection. Q. Rev. Biol. 53:101–114.

Wade, M. J., and D. E. McCauley. 1988. Extinction and colonization: their effects on the genetic differentiation among populations. Evolution 42:995–1005.

Wagner, P. J., and D. H. Erwin. 1995. Phylogenetic patterns as tests ofspeciation models. Pp. 87–122 *in* D. H. Erwin and R. L. Anstey, eds. New approaches to speciation in the fossil record. Columbia Univ. Press, New York.

Wake, D. B. 1997. Incipient species formation in salamanders of the *Ensatina* complex. Proc. Natl. Acad. Sci. USA 94: 7761–7767.

Walsh, J. B. 1982. Rate of accumulation of reproductive isolation by chromosome rearrangements. Am. Nat. 120:510–532.

Whitlock, M. C., and D. E. McCauley. 1990. Some population genetic consequences of colony formation and extinction: genetic correlation within founding groups. Evolution 44:1717–1724.

Whitlock, M. C., P. C. Phillips, and M. J. Wade. 1993. Gene interaction affects the additive genetic variance in subdivided populations with migration and extinction. Evolution 47:1758–1769.

Wright, S. 1940. Breeding structure of populations in relation to speciation. Am. Nat. 74:232–248.

———. 1978. Evolution and the genetics of populations. Vol. 4. Variability within and among natural populations. The Univ. of Chicago Press, Chicago, IL.

Wu, C.-I., and M. F. Palopoli. 1994. Genetics of postmating reproductive isolation in animals. Annu. Rev. Genet. 27:283–308.

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APPENDIX

First we estimate the probability s that two neighboring demes, say, x and y, belong to different species. Looking back in time, these two demes canbe traced to a single founding deme τ generations ago. Using a coalescing random-walk system on a one-dimensional lattice in which walks move to either neighboring site with probability $\delta/2$ and coalesce when they meet, we find the probability distribution of the time τ until the first common ancestor is asymptotically

$$P(\tau \geq t) \sim \frac{1}{\sqrt{\delta \pi t}} \tag{A1}$$

(e.g., Kelly 1977; cf. Bramson et al. 1996). Demes x and y belong to different species if they have accumulated K mutations since time τ generations ago. With small μ, the process of mutation accumulation is Poisson. We will use $X(\lambda)$ to denote a generic Poisson(λ) random variable. Therefore, the probability that x and y are different species is

$$s = P[X(2\mu\tau) \geq K] = \sum_{t} P[X(2\mu t) \geq K]P(\tau = t), \tag{A2}$$

which is (for small δ and μ/δ) approximated by

$$\frac{1}{2\sqrt{\delta\pi}} \int_0^\infty P[X(2\mu t) \geq K] t^{-3/2}\, dt. \tag{A3}$$

Because

$$P[X(t) \geq a] = \int_0^t P[X(u) = a - 1]\, du, \tag{A4}$$

we get, for $b > 1$ and $a > b - 1$,

$$\begin{aligned} \int_0^\infty P[X(t) \geq a] t^{-b}\, dt &= \frac{1}{b-1} \int_0^\infty t^{1-b} P[X(t) = a - 1]\, dt \\ &= \frac{\Gamma(a - b + 1)}{(b - 1)(a - 1)!}. \end{aligned} \tag{A5}$$

Therefore, the asymptotic density of borders between different species is, for a fixed K,

$$s = \sqrt{\frac{2\mu}{\pi\delta}} \cdot \frac{\Gamma(K - 1/2)}{(K - 1)!}. \tag{A6}$$

The last factor is asymptotic to $K^{-1/2}$ for large K.

Equation (3).—The average range size, R, of a species is the inverse of s.

Equation (4).—The average number of species, S, in the system is sn.

Equation (5).—First we give a qualitative argument why T is of the order μ/K. Species extinction is represented by the collision of two species borders. The dynamics of species borders can be modeled as a random walk on a one-dimensional lattice with the diffusion coefficient $\delta/2$. To move distance L, it takes order $L^2/(\delta/2)$ time steps. Because the average distance between borders is R, they will collide on average in order $R^2/(\delta/2)$ time steps. The rate of collision (turnover rate, T) is the inverse of this, resulting in the turnover rate order μ/K. A more rigorous derivation based on a consideration of the process of creation and annihilation of borders leads to the conclusion that for $K \geq 2$,

$$T = \frac{\mu}{K - 3/2} - \text{some smaller terms.} \tag{A7}$$

For $K = 1$, the turnover rate is asymptotically

$$T = \sqrt{\frac{2\delta}{\mu}}, \tag{A8}$$

which is quite different than for $K > 1$.